Reorganization in complex landscapes: causes and consequences of changes in meta-food-webs

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Summary

What are the ecological impacts of global change on complex communities like food webs? What happens when the balance in an ecosystem is disturbed and why are some species more likely to go extinct than others? These are extremely important and timely issues considering the unprecedented species extinction rates we are currently observing, resulting in the rapid loss of global biodiversity. Most of this loss can be attributed to human activities like land use changes causing the fragmentation and loss of habitat, overharvesting, pollution, and the introduction of invasive alien species (for example, new predators or competitors). The correlation between human activities and the current biodiversity crisis is well established, yet we lack a clear mechanistic understanding of what governs the ecological responses of whole ecosystems to these global changes. This is, in part, because we lack a thorough understanding of the ecological processes, like species interactions and dispersal, that mediate these responses and their variability in realistically complex ecosystems.

These ecological processes are highly complex and involve multiple interacting species that move freely about the landscapes and thus, understanding these processes demands measures that can account for this complexity, at both the local and landscape scale. So far, such measures are however scarce, as different groups of ecologists traditionally study these key ecological processes. Firstly, food web ecology, characterizing the diversity of species and their (feeding) interactions within local ecosystems. While food web ecology can account for a large number of biotic interactions in local ecosystems, it typically ignores aspects of spatial scale. In nature, food web dynamics are however not restricted to local ecosystems but determined by interactions within and between species and between species and their environment across habitat boundaries. By neglecting the potentially strong impact that spatial aspects can have on (local) communities, food web ecology is limited in its ability to accurately predict food web responses in the context of global change. Secondly, metacommunity ecology describes the dispersal dynamics between local communities (of interacting species) but does

not address food web complexity. However, global change directly affects abiotic conditions and living organisms, impinging on all trophic levels and spatial scales. In this thesis, I fill this scientific gap by bridging these two core fields of ecology and combine the local population dynamics of complex food webs and their metacommunity (i.e., dispersal) dynamics. Analyzing food webs in a metacommunity context (so called meta-food-webs) allows me to incorporate real-world complexity for both local and spatial processes to examine how food webs respond to global change. I primarily focus on land use changes that alter the spatial configuration of habitats, like habitat loss and fragmentation. To approach these aims, I propose new theoretical frameworks in which I combine ecology and mathematics to delve into the underlying mechanisms governing the impacts of global changes on multitrophic communities in complex landscapes, and to explore variations in these responses among species, trophic groups, landscapes and global change drivers.

In research chapter 1, I ask to what extent trophic interactions and dispersal dynamics influence the persistence of species in meta-food-webs when landscapes become increasingly fragmented. I focus specifically on identifying species and trophic groups that have higher extinction risks which then may result in a reorganization of the meta-food-web at the landscape scale. I do so by integrating a bioenergetic food web model and a spatial network model that both use allometric scaling relationships of trophic and, respectively, spatial processes as a unifying principle into a meta-food-web model. This means both models employ body mass as a 'super trait' that fully characterizes each species, yielding a model that follows allometric scaling laws for metabolism, growth, feeding and dispersal. By explicitly modelling the local population dynamics between species and the spatial dispersal dynamics between local populations, this method can account for both the direct and indirect effects arising from these processes. Thus, it offers a highly detailed description of trophic communities, allowing me to explore the local and spatial processes underpinning the species diversity patterns in multitrophic metacommunities in response to habitat fragmentation (i.e, specifically, the number of habitat patches and their degree of isolation). I identify habitat isolation as the key driver for species loss and diversity decline. Moreover, I show that large-bodied consumer species at high trophic positions have an elevated extinction risk due to bottom-up energy limitation if landscapes become increasingly isolated, despite being superior dispersers that connect fragmented landscapes better. These findings provide strong evidence for interacting processes of local and spatial dynamics (i.e, trophic interactions and dispersal) that mediate the response of complex communities like food webs to alterations of the landscape structure.

In research chapter 2, I test how different scenarios of progressive habitat loss affect species extinction rates in even larger meta-food-webs. To this end, I combine classic metapopulation models

on fragmented landscapes with a Bayesian network representation of food webs for calculating local species' extinction rates. This method offers the capability to examine trophic metacommunities with hundreds of species and patches and to explore variations in species extinction rates in response to different scenarios of progressive habitat loss, varying in whether one prioritizes the removal of valuable vs. non-valuable patches. To assess the value of a patch I repurpose known results from classic metapopulation theory for trophic metacommunities, which allows me to rank patches with respect to their importance to the persistence of the metacommunity as a whole. I employ this patch ranking to examine the effects of habitat loss, both on model communities and as a case study the plant-mammal Serengeti food web dataset, an iconic but highly threatened system. The results show that metacommunity persistence depends on the order of habitat removal. If patches which are least crucial to persistence are removed first (best-case scenario), the metacommunities can often tolerate the removal of more than 90% of their patches. On the other hand, focusing on removing the most crucial patches first (worst-case scenario), very quickly leads to the collapse of metacommunities. Interestingly, this also applies to removing patches at random, which is nearly indistinguishable in its effects from the worst-case scenario as both cases result in highly fragmented and isolated landscapes (in contrast to the best-case scenario). In all scenarios, I find that species' vulnerability to habitat loss is greater at higher trophic levels, a pattern which is (mostly) independent of model parameterization, emphasizing the generality of these trends. This also holds true for the patterns I find for the plant-mammal Serengeti food web dataset, which demonstrates that this framework can be readily applied to empirical systems. These findings reinforce the results showing the higher extinction risks of top species with increasing habitat isolation that I found in research chapter 1. In summary, this indicates that species at high trophic positions might go extinct more quickly than species at lower trophic positions considering globally progressing land use changes that cause the destruction of habitat and often result in increasingly fragmented landscapes (e.g., due to agricultural intensification). The elevated extinction risk of species at high trophic positions poses a severe threat to trophically complex metacommunities and may lead to communities with fewer species and less trophic complexity.

Building on the establishment that food web responses to land use changes are mediated by species interactions and dispersal dynamics, and the important role ot the spatial distribution of habitat, in research chapter 3, I study the combined effects of multiple global change drivers: land use changes and invasive alien species. Both are major components of global change that have been shown to collectively threaten biodiversity and cause biotic homogenization. However, an outstanding problem with understanding the joint effects of land use changes and biological invasions concerns our ability

to predict which combinations of species, environmental conditions and landscape structures most effectively facilitate or prevent biological invasions. Biological invasions are complex processes that consist of several stages (introduction, establishment, and subsequent spread). When and where alien species will successfully invade a new environment thus involves a complex combination of interacting factors. It is well established that landscape structures, as well as the state and the structure of the resident community (for example, food web topology) play a key role in determining whether an alien species becomes invasive but our understanding of how these factors interact remains limited. Considering the recent increases of invasive alien species, like insects, algae and crustaceans, that often have been introduced through trade and the transport of goods and people, understanding which combinations of species, environmental conditions and landscape structures promote biological invasions is of urgent need. In research chapter 3, I contribute to filling this gap by testing which landscape properties underlying the local and spatial processes of food webs mediate biological invasions, and to what extent the emerging patterns are shaped by invasive species traits. To test this, I develop a holistic network-based approach that is built on the bioenergetic meta-food-web model from research chapter 1 and includes single-species invasions by animal and plant species in landscapes varying in their landscape structure (i.e., clustered and random distribution of habitat) and environmental conditions (i.e., levels of nutrient supply). This addition allows me to explore which landscape properties underlying the local and spatial processes of food webs mediate biological invasions, and to what extent the emerging patterns are shaped by invasive species traits. I find that knowledge of the spatial network structure is crucial to accurately predict biological invasions, and in particular the further spread of an invader across a new environment, provided there is sufficient nutrient supply in the landscape. The latter applies predominantly to species at high trophic positions whose persistence relies on sufficient energy supply in the landscape. Also, I show that good dispersal abilities can generally promote the spread of invasive species. Thereby, this framework clearly demonstrates that biological invasions are mediated by the interplay between landscape properties, resident food webs, and invasive species. As such, this study contributes to a better understanding of the combined factors determining biological invasions, and can aid ecologists to more effectively predict and manage biological invasions.

Overall, in this I thesis I demonstrate that local and spatial processes mediate meta-food-web responses to global change. Specifically, I illustrate that there is a strong trophic dependency in the response of species to land use changes and emphasize that especially (large-bodied) consumer species at high trophic positions have elevated extinction risks when habitat becomes increasingly isolated (research chapters 1 and 2). Considering the projected land use changes, these findings stress

the risk of network downsizing, yielding food webs with fewer species and less trophic complexity. Finally, in research chapter 3, by jointly considering multiple aspects of global change, I demonstrate the interdependence of these different environmental stressors. Moreover, by incorporating real-world complexity for the first time in models that synthesize two key ecological processes (trophic interactions and dispersal between habitats), this thesis significantly advances our mechanistic understanding of how these processes govern the response of complex ecosystems to global changes. Therefore, it presents a major step towards a clearer understanding of food web responses to global change impacts. These important insights for community ecology would not have been revealed without an analysis of complex communities at different levels of biological organization and spatial scales, highlighting key areas for future theoretical explorations and empirical research. An important outcome of collective dynamics in natural ecosystems will depend on how species traits influence the organization of complex ecological networks that span across habitat boundaries. In summary, this thesis provides an important contribution to better predict and manage future biodiversity change in natural ecosystems.

Zusammenfassung

Was sind die ökologischen Auswirkungen des globalen Wandels auf komplexe Artengemeinschaften wie Nahrungsnetze? Was passiert, wenn das Gleichgewicht in einem Ökosystem gestört wird und warum sterben einige Arten eher aus als andere? Dies sind äußerst wichtige und dringende Fragen angesichts der beispiellosen Aussterberaten, die wir derzeit beobachten und die zu einem drastischen Verlust der globalen Biodiversität führen. Der größte Teil dieses Verlustes kann auf menschliche Aktivität zurückgeführt werden, wie Landnutzungsänderungen, die zur Fragmentierung und zum Verlust von Lebensraum führen, der Ausbeutung natürlicher Ressourcen, Umweltverschmutzung sowie der Einführung invasiver gebietsfremder Arten. Der Zusammenhang zwischen menschlichen Aktivitäten und dem gegenwärtigen Biodiversitätsverlust ist gut erforscht, doch uns fehlt ein klares mechanistisches Verständnis dessen, was die ökologischen Reaktionen ganzer Ökosysteme auf diese Veränderungen bestimmt. Dies liegt unter anderem daran, dass uns ein grundlegendes Verständnis der ökologischen Prozesse, wie Interaktionen zwischen Arten und deren Ausbreitung, fehlt, die diese Reaktionen und ihre Variabilität in komplexen Ökosystemen vermitteln.

Diese ökologischen Prozesse sind hochkomplex und umfassen eine Vielzahl interagierender Arten, die sich frei in der Landschaft bewegen. Daher erfordert das Verständnis dieser Prozesse Maßnahmen, die dieser Komplexität sowohl auf lokaler als auch auf landschaftlicher Ebene Rechnung tragen können. Bisher sind solche Maßnahmen jedoch kaum vorhanden, da traditionell verschiedene Gruppen von Ökologinnen und Ökologen diese Schlüsselprozesse untersuchen. Die Ökologie der Nahrungsnetze charakterisiert die Vielfalt der Arten und ihre (Fraß-)Interaktionen innerhalb lokaler Ökosysteme. Damit kann die Ökologie der Nahrungsnetze zwar eine große Anzahl biotischer Interaktionen in lokalen Ökosystemen erklären, ignoriert aber in der Regel Landschaftsaspekte. In der Natur ist die Dynamik von Nahrungsnetzen jedoch nicht auf lokale Ökosysteme beschränkt, sondern wird durch Interaktionen innerhalb und zwischen Arten sowie zwischen Arten und ihrer Umwelt

über Habitatgrenzen hinweg bestimmt. Durch die Vernachlässigung der potenziell starken Auswirkungen, die räumliche Aspekte auf (lokale) Artengemeinschaften haben können, ist die Ökologie der Nahrungsnetze in ihrer Fähigkeit, genau vorherzusagen, wie Nahrungsnetze auf Umweltveränderungen reagieren, eingeschränkt. Andererseits beschreibt die Ökologie der Meta-Gemeinschaften die Ausbreitungsdynamik zwischen lokalen Gemeinschaften (interagierender Arten), geht aber nicht auf die Komplexität der Nahrungsnetze ein. Der globale Wandel wirkt sich jedoch direkt auf abiotische Bedingungen und lebende Organismen aus und zwar auf allen trophischen Ebenen und räumlichen Skalen. In dieser Arbeit schließe ich diese Wissenslücke, indem ich beide Kernbereiche der Ökologie zusammenführe und die lokalen Populationsdynamiken komplexer Nahrungsnetze und ihre Ausbreitungsdynamiken auf Landschaftsebene miteinander verbinde. Die Analyse von Nahrungsnetzen in einem Meta-Gemeinschafts-Kontext (d. h. Meta-Nahrungsnetze) erlaubt es mir, die Komplexität der Natur sowohl für lokale als auch für räumliche Prozesse einzubeziehen, um zu untersuchen, wie Nahrungsnetze auf Umweltveränderungen reagieren. Dabei konzentriere ich mich vor allem auf Landnutzungsänderungen, die die räumliche Konfiguration von Lebensräumen verändern, wie Habitatverlust und Fragmentierung. Dazu entwickle ich neue theoretische Modelle, in denen ich Ökologie und Mathematik kombiniere, um die zugrunde liegenden Mechanismen zu erforschen, die die Auswirkungen des globalen Wandels auf multitrophe Gemeinschaften in komplexen Landschaften steuern und um Unterschiede in den Reaktionen zwischen Arten, trophischen Gruppen, Landschaften und Umweltveränderungen zu erforschen.

In Forschungskapitel 1 untersuche ich, inwieweit trophische Interaktionen und Ausbreitungsdynamik die Persistenz von Arten in Meta-Nahrungsnetzen beeinflussen, wenn Landschaften zunehmend fragmentiert werden. Ich konzentriere mich speziell auf die Identifizierung von Arten und trophischen Gruppen, die ein höheres Aussterberisiko haben, was dann zu einer Reorganisation des Meta-Nahrungsnetzes auf Landschaftsebene führen kann. Dazu integriere ich Nahrungsnetzmodelle und räumliche Netzwerke, die allometrische Skalierungsbeziehungen trophischer und räumlicher Prozesse als vereinheitlichendes Prinzip verwenden, in ein Meta-Nahrungsnetz-Modell. Das bedeutet, dass beide Modelle Körpermasse als “Super-Merkmal” verwenden, das jede Art vollständig charakterisiert, was zu einem Modell führt, das allometrischen Skalierungsgesetzen für Metabolismus, Art-Interakionen und Ausbreitung folgt. Durch die explizite Modellierung der lokalen Populationsdynamiken zwischen Arten und der räumlichen Ausbreitungsdynamik zwischen lokalen Populationen kann diese Methode sowohl die direkten als auch die indirekten Auswirkungen dieser Prozesse berücksichtigen. Auf diese Weise bietet sie eine sehr detaillierte Beschreibung der trophischen Artengemeinschaften. Dies ermöglicht es mir, die lokalen und räumlichen Prozesse zu untersuchen,

die den Mustern der Artenvielfalt in multitrophischen Meta-Gemeinschaften als Reaktion auf die Lebensraumfragmentierung zugrunde liegen (d. h. insbesondere die Anzahl der Habitate und den Grad ihrer Isolation). Ich identifiziere die Habitatisolation als die Hauptursache für den Verlust von Arten. Darüber hinaus zeige ich, dass große und schwere Tierarten an hohen trophischen Positionen ein erhöhtes Aussterberisiko haben, da ihnen nicht genügend Ressourcen zur Verfügung stehen um ihren hohen Energiebedarf zu decken, wenn die Isolation der Landschaften zunimmt. Dies geschieht, obwohl sie durch ihre höhere Ausbreitungsfähigkeit fragmentierte Landschaften besser miteinander verbinden können. Diese Ergebnisse liefern starke Hinweise auf interagierende Prozesse lokaler und räumlicher Dynamiken (d. h. trophische Interaktionen und Ausbreitungsprozesse), die die Reaktion komplexer Artengemeinschaften wie Nahrungsnetze auf Landnutzungsänderungen bestimmen.

In Forschungskapitel 2 teste ich, wie verschiedene Szenarien des fortschreitenden Habitatverlusts die Aussterberate von Arten in noch größeren Meta-Nahrungsnetzen beeinflussen. Zu diesem Zweck kombiniere ich klassische Metapopulations-Modelle auf fragmentierten Landschaften mit einer Bayes'schen Netzwerkdarstellung von Nahrungsnetzen zur Berechnung der lokalen Aussterberaten von Arten. Diese Methode bietet die Möglichkeit, trophische Meta-Gemeinschaften mit Hunderten von Arten und Habitaten zu untersuchen und Unterschiede in den Aussterberaten als Reaktion auf verschiedene Szenarien des fortschreitenden Habitatverlusts zu erforschen. Die Szenarien unterscheiden sich darin, ob zuerst wertvolles oder nicht wertvolles Habitat verloren geht. Dazu verwende ich bekannte Ergebnisse der klassischen Metapopulationstheorie für trophische Meta-Gemeinschaften, was es mir ermöglicht, Habitate nach ihrer Bedeutung für die Persistenz der Meta-Gemeinschaft als Ganzes zu ordnen. Diese Rangfolge der Habitate nutze ich, um die Auswirkungen des Habitatverlusts, sowohl auf Modellnahrungsnetze als auch auf das Serengeti-Nahrungsnetz, ein einzigartiges, aber hochgradig bedrohtes System, zu untersuchen. Die Ergebnisse zeigen, dass die Persistenz der Meta-Gemeinschaft von der Reihenfolge des Habitatverlusts abhängt. Wenn Habitate, die für die Persistenz am wenigsten entscheidend sind, zuerst entfernt werden (Best-Case-Szenario), können die Meta-Gemeinschaften oft die Entfernung von mehr als 90% der Habitate in einer Landschaft tolerieren. Werden die wichtigsten Habitate jedoch zuerst entfernt (Worst-Case-Szenario), führt dies sehr schnell zum Zusammenbruch der Meta-Gemeinschaften. Interessanterweise gilt dies auch für die zufällige Entfernung von Habitaten, die sich in ihren Auswirkungen kaum vom Worst-Case-Szenario unterscheiden lässt, da beide zu stark fragmentierten und isolierten Landschaften führen (im Unterschied zum Best-Case-Szenario). In allen Szenarien stelle ich fest, dass die Anfälligkeit der Arten für Habitatverlust auf höheren trophischen Ebenen größer ist, ein Muster, das größtenteils unabhängig von der Modellparametrisierung ist, was die Allgemeingültigkeit dieser Trends unterstreicht. Dies gilt

auch für die Muster, die ich für das Serengeti-Nahrungsnetz finde, was zeigt, dass diese Methode leicht auf empirische Systeme angewandt werden kann. Dies unterstützt die Ergebnisse aus Forschungskapitel 1, die ein höheres Aussterberisiko von Top-Arten mit zunehmender Lebensraumisolierung zeigen. Dies deutet darauf hin, dass mit fortschreitende Landnutzungsänderung Arten in hohen trophischen Positionen schneller aussterben könnten als Arten in niedrigeren trophischen Positionen. Das erhöhte Aussterberisiko von Arten in hohen trophischen Positionen stellt eine ernste Bedrohung für trophisch komplexe Meta-Gemeinschaften dar und kann zu Gemeinschaften mit weniger Arten und weniger trophischer Komplexität führen.

Aufbauend darauf, dass die Reaktionen komplexer Nahrungsnetze auf Landnutzungsänderungen von den Interaktionen zwischen Arten und ihren Ausbreitungsdynamiken sowie der räumlichen Verteilung von Habitat abhängen, untersuche ich im Forschungskapitel 3 das Zusammenwirken mehrerer Faktoren des globalen Wandels: Landnutzungsänderungen und invasive gebietsfremde Arten. Beides sind Hauptkomponenten des globalen Wandels, die nachweislich gemeinsam die biologische Vielfalt bedrohen und eine biotische Homogenisierung bewirken können. Die gemeinsamen Auswirkungen von Landnutzungsänderungen und biologischen Invasionen lassen sich allerdings nur schwer vorhersagen, da wir nur wenig darüber wissen, welche Kombinationen von Arten, Umweltbedingungen und Landschaftsstrukturen biologische Invasionen einerseits erleichtern oder aber verhindern können. Biologische Invasionen sind komplexe Prozesse, die aus mehreren Phasen bestehen (Einführung, Etablierung und anschließende Ausbreitung). Wann und wo gebietsfremde Arten erfolgreich in eine neue Umwelt eindringen werden, ist somit eine komplexe Kombination von interagierenden Faktoren. Es ist allgemein bekannt, dass Landschaftsstrukturen sowie der Zustand und die Struktur der ansässigen Artengemeinschaft (z. B. die Topologie des Nahrungsnetzes) eine Schlüsselrolle bei der Entscheidung spielen, ob eine gebietsfremde Art invasiv wird, aber unser Verständnis darüber, wie diese Faktoren interagieren, ist bisher begrenzt. In Anbetracht der jüngsten Zunahme invasiver gebietsfremder Arten wie Insekten, Algen und Krebstiere, die häufig durch Handel und Transport von Waren und durch Menschen eingeschleppt wurden, ist es dringend erforderlich zu verstehen, welche Kombinationen von Arten, Umweltbedingungen und Landschaftsstrukturen die Ausbreitung invsasiver Arten begünstigen. In Forschungskapitel 3 trage ich dazu bei, diese Wissenslücke zu schließen, indem ich untersuche, welche Landschaftseigenschaften, die den lokalen und räumlichen Prozessen der Nahrungsnetze zugrunde liegen, biologische Invasionen begünstigen und inwieweit die entstehenden Muster durch Merkmale invasiver Arten geprägt sind. Um dies zu testen, entwickle ich einen ganzheitlichen netzwerkbasierten Ansatz, der auf das bioenergetischen Meta-Nahrungsnetz-Modell aus Forschungskapitel 1 aufbaut und Invasionen einzelner Tier- und Pflanzenarten in Landschaften simu-

liert, die sich in ihrer Landschaftsstruktur (d. h. geklumpte und zufällige Verteilung des Lebensraums) und in ihren Umweltbedingungen (d. h. in der Höhe der Nährstoffversorgung) unterscheiden. Diese Ergänzung erlaubt es mir zu untersuchen, welche Landschaftseigenschaften, die den lokalen und räumlichen Prozessen der Nahrungsnetze zugrunde liegen, biologische Invasionen verstärken können und inwieweit die entstehenden Muster durch Merkmale invasiver Arten geprägt sind. Die räumliche Netzstruktur ist von entscheidender Bedeutung um die erfolgreiche Etablierung und weitere Ausbreitung einer invasiven Art in einer neuen Umgebung genau vorherzusagen zu können, vorausgesetzt, es gibt eine ausreichende Nährstoffversorgung in der Landschaft. Letzteres gilt vor allem für Arten in hohen trophischen Positionen, deren Fortbestand von einer ausreichenden Energieversorgung in der Landschaft abhängt. Ich zeige auch, dass ein gutes Ausbreitungsvermögen die Ausbreitung invasiver Arten begünstigt. Damit zeigt diese Studie deutlich, dass biologische Invasionen durch das Zusammenspiel von Landschaftseigenschaften, den ansässigen Nahrungsnetzen und invasiven Arten vermittelt werden. Als solches trägt diese Studie zu einem besseren Verständnis der Faktoren bei, die biologische Invasionen bestimmen, und kann Ökologinnen und Ökologen dabei helfen, biologische Invasionen effektiver vorherzusagen und so gegebenfalls auch zu verhindern.

Insgesamt zeige ich in dieser Arbeit, dass die Reaktionen von Meta-Nahrungsnetzen auf globale Umweltveränderungen von lokalen und räumlichenn Prozesse abhängen. Insbesondere zeige ich auf, dass die Reaktion von Arten auf Landnutzungsänderungen stark von ihrer trophischen Position abhängt und insbesondere (große und schwere) Tierarten an hohen trophischen Positionen ein erhöhtes Aussterberisiko haben, wenn Lebensräume zunehmend isoliert werden (Forschungskapitel 1 und 2). In Anbetracht der prognostizierten Landnutzungsänderungen betonen diese Ergebnisse das Risiko einer Verkleinerung des Netzes, d. h. hin zu Nahrungsnetzen mit weniger Arten und geringerer trophischer Komplexität. Weiterhin zeige ich in Forschungskapitel 3, indem ich gemeinsam mehrere Aspekte des globalen Wandels betrachte, die Interdependenz dieser verschiedenen Umweltstressoren auf. Durch die erstmalige Einbeziehung natürlicher Komplexität in Modelle, die zwei ökologische Schlüsselprozesse (d. h. trophische Interaktionen und Ausbreitung zwischen Lebensräumen) verknüpfen, trägt diese Arbeit zudem wesentlich zu unserem (mechanistischen) Verständnis bei, wie diese Prozesse die Reaktion komplexer Ökosysteme auf den globalen Wandel steuern. Daher stellt sie einen wichtigen Schritt hin zu einem klareren mechanistischen Verständnis der Reaktionen von Nahrungsnetzes auf die Auswirkungen des globalen Wandels dar. Diese wichtigen Erkenntnisse für die Ökologie von Artengemeinschaften wären ohne eine Analyse komplexer Gemeinschaften auf verschiedenen Ebenen der biologischen Organisation und auf räumlichen Skalen nicht möglich gewesen. Sie heben Schlüsselbereiche für künftige theoretische und empirische Forschung hervor.

Ein wichtiges Ergebnis der kollektiven Dynamik in natürlichen Ökosystemen wird davon abhängen, wie die Eigenschaften der Arten die Organisation komplexer ökologischer Netzwerke beeinflussen, die sich über Lebensraumgrenzen hinweg erstrecken. Zusammenfassend lässt sich sagen, dass diese Arbeit einen wichtigen Beitrag zur besseren Vorhersage künftiger Veränderungen der biologischen Vielfalt in natürlichen Ökosystemen leistet und dazu beitragen kann, die biologische Vielfalt zu erhalten.

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I

General Introduction

1 | Understanding the current biodiversity crisis and its driving forces

1.1 What we know

The rapid growth of the human population has led to an increasing demand for natural resources but meeting these demands exerts high pressures on (natural) ecosystems. Today, most ecosystems are already heavily degraded by the aggregated impacts of human activities, often with catastrophic consequences for biodiversity (Sala et al., 2000; IPBES, 2019). Over the last decades, the extraction of biomass, fossil fuels, minerals, and metals has increased approximately by 80%, urban area has doubled since 1992, and agricultural area has been significantly expanded (mostly into tropical forests) and intensified (Zalasiewicz et al., 2011; IPBES, 2019). These changes in land use are key components of global change and have by far the most severe impacts on terrestrial ecosystems (Sala et al., 2000; IPBES, 2019). In a prominent global change study, Sala et al. (2000) conclude that land use change will be the global change driver with the most devastating effects on global biodiversity by the year 2100. The authors attribute these detrimental impacts to agricultural expansion and intensification causing the rapid loss and fragmentation of suitable habitat, and consequently species extinctions. Besides the changes in the spatial configuration of habitat (i.e., landscape structure), agricultural intensification often entails heavy fertilizer input, which can alter nutrient cycles and thereby also population and community dynamics (Tilman et al., 2002; MEA, 2005; Schweiger et al., 2005). In many ecosystems, human activities have also led to high rates of biotic exchange (Chen et al., 2011; Van Kleunen et al., 2015), and the number of invasive alien species has increased substantially over the last 50 years (Seebens et al., 2017; IPBES, 2019). Biological invasions often cause vast shifts in the composition of native communities, giving rise to the concern that the Earth's biota may become more and more homogenized (Courchamp et al., 2017; Ricciardi et al., 2017). Collectively, these factors have accelerated species extinction rates towards unprecedented levels, and we are currently in the midst of the sixth mass extinction crisis (Pimm et al., 1995; Dirzo and Raven, 2003; Barnosky et al., 2011; Ceballos et al., 2015, 2017). In contrast to previous mass extinction events, for instance, the extinction of dinosaurs due to sudden changes in the physical environment caused by meteor impacts, the current one is driven by human activities (Dirzo and Raven, 2003). This correlation of the current biodiversity crisis with human activities is well established (see, for example, Sala et al., 2000; Dirzo and Raven, 2003; Barnosky et al., 2011; Pimm et al., 2014; Ceballos et al., 2015, 2017).

Land use changes Human land use is reshaping landscapes (Haddad et al., 2015) and these land use changes entail dramatic consequences for populations and species but also for functional diversity,

community composition, species interactions, ecosystem functioning as well as human wellbeing (see, for example, Chapin et al., 2000; Sala et al., 2000; MEA, 2005; Pereira et al., 2010; Barnosky et al., 2011; Cardinale et al., 2012; Pimm et al., 2014; Valiente-Banuet et al., 2015; Ceballos et al., 2015, 2017). Above all, the expansion and intensification of agricultural area but also forestry and urbanization cause the destruction, degradation, and fragmentation of natural habitats (Haddad et al., 2015; IPBES, 2019). This often results in a division of suitable habitat into smaller and more isolated habitat fragments separated by a matrix of human-transformed landscape cover (in short, the habitat matrix) (Prugh et al., 2008; Franklin and Lindenmayer, 2009). These fragments are then often even more exposed to human land use (Fahrig, 2003; Haddad et al., 2015) and also the habitat matrix strongly varies in its degree of suitability (Prugh et al., 2008; Franklin and Lindenmayer, 2009). These alterations of natural landscapes can affect ecosystems through a variety of mechanisms by altering the configuration and quality of habitat as well as the habitat matrix conditions, impinging on all trophic levels (Van Nouhuys, 2005; Tylianakis et al., 2007; Martinson and Fagan, 2014). With landscapes becoming increasingly fragmented and patchy, local populations are often more likely to go extinct and thus species persistence at the metapopulation or metacommunity level critically depends on dispersal (Levins, 1969; Hanski, 1998; Grilli et al., 2015). Furthermore, agricultural intensification but also forestry and urbanization often entail the pollution of air, water and soil (IPBES, 2019; Bowler et al., 2020). For example, agriculture intensification processes have been found to dramatically increase nitrogen deposition with devastating impacts on biodiversity (De Schrijver et al., 2011; Bowler et al., 2020) and are often accompanied with heavy pesticide use (Geiger et al., 2010). In the long term, however, agricultural intensification may also cause nutrient deprivation (Vitousek et al., 2009).

Invasive alien species The conversion of natural to human-dominated landscapes not only has direct impacts on resident species, but often also increases the likelihood of species invasions (Didham et al., 2007). Invasive alien species are a major threat to global biodiversity and ecosystem functioning and recently, an increasing number of alien species of taxa, such as insects, algae and crustaceans, have been introduced through trade and the transport of goods and people (Seebens et al., 2017; IPBES, 2019; Roy et al., 2019; Bowler et al., 2020). Although so far invasive alien species have lower relative impacts compared to land use change, their numbers are accelerating, as shown in a recent analysis of a global database (Seebens et al., 2017). This applies for alien species across all taxonomic groups and is majorly driven by globalization, human transport and trade, by accident or intention (see, e.g., Courchamp et al., 2017; Seebens et al., 2017; Frost et al., 2019). One prominent example is the Harlequin ladybird, *Harmonia axyridis* (Pallas), a species native to central and East Asia that

in many countries has been intentionally introduced as a biological control, which then, however, has rapidly spread all over North America and Europe starting in the late 1980s (Lombaert et al., 2010; Stanković et al., 2011; Roy et al., 2016). In these countries, as a generalist top predator it poses a severe threat to the native biodiversity through competition and predation, especially for aphidophagous insects (Roy et al., 2016). Furthermore, in many island countries, invasive alien species have significantly reduced native biodiversity and often are the key driver of species extinctions (Clergeau and Mandon-Dalger, 2001; Benning et al., 2002; Dirzo and Raven, 2003; IPBES, 2019). This exemplifies that biological invasions can have profound consequences for native communities and may drastically alter community composition.

Moreover, although global change drivers have received a lot of attention, they are often presented individually, as separated effects but they do not act in this way. They interact with each other with synergistic but also antagonistic effects (Vitousek, 1994; Didham et al., 2007; Ficetola et al., 2010; Binzer et al., 2012, 2016; Northrup et al., 2019), and the strength of these effects can strongly determine how natural ecosystems respond to these global changes. This has been illustrated for example by Benning et al. (2002), who showed that replacing the forest habitat of the Hawaiian honeycreepers (Drepanidae) with crop and pasture land, and the introduction of predators and diseases by humans, quickly drove the majority of honeycreeper species towards extinction. The remaining species are at the brink of extinction due to the combined effects of anthropogenic climate change, land use changes and biological invasions.

1.2 What we do not know

Although the correlation between human activities and the current biodiversity crisis has been established for decades, accurately predicting biodiversity responses to global changes remains challenging. This is, in part, because studies addressing this topic primarily have focused on the loss of species, and have for the most part neglected the ecological processes that mediate this loss, like species interactions and dispersal (Tylianakis et al., 2008; Valiente-Banuet et al., 2015). As a consequence, a clear (mechanistic) understanding of how these processes mediate species loss and biodiversity change is lacking, particularly for complex ecosystems. With further environmental changes projected over the next years, understanding ecosystems responses to these changes and the underlying ecological mechanisms and processes is of urgent need to improve predictions and for guiding conservation efforts.

In this thesis, I address this challenge by advancing the mechanistic understanding of ecosystem responses to global change, primarily focusing on land use changes that alter the spatial configuration

of habitats, like habitat loss and fragmentation. To this end, I merge two core but mostly independent and separate fields of ecology that address two types of ecological processes: (1) food web ecology, characterizing the diversity of species and their (feeding) interactions within local ecosystems (Dunne, 2005; Bascompte, 2009); and (2) metacommunity ecology, describing the dispersal dynamics between a set of local communities (of interacting species) (Leibold et al., 2004; Holyoak et al., 2005). Whereas the latter for the most part does not address food web complexity, although metacommunity models play a central role in unifying theories of biodiversity (see the review by Guzman et al., 2018 and references therein), food web ecology usually ignores aspects of spatial scale, and thereby also the potentially strong impact that spatial aspects can have on (local) communities (Polis et al., 1997; Gibert and Yeakel, 2019). Understanding food web responses to global change impacts at different levels of biological organization and spatial scales can yield important insights for community ecology and conservation biology. This is of urgent need for the maintenance of trophically complex communities and for improving predictions and conservation strategies to manage the current biodiversity crisis. By addressing this important and timely topic, I strive to conceptualize the understanding of collective dynamic phenomena in natural ecosystems organized in complex ecological networks across spatial scales in the context of global change.

2 | Food webs

2.1 From trophic interactions to food webs

The ways in which species can interact are highly numerous and complex, with predation, mutualism, competition, and parasitism being perhaps the most prominent examples (Montoya et al., 2006; Bascompte, 2009; McCann and Rooney, 2009; Kéfi et al., 2012). In this thesis, I focus on predation, or more generally speaking feeding (or trophic) interactions, i.e., who eats whom. Trophic interactions have found longstanding applications in ecological studies as they represent the fluxes of energy and matter trough ecosystems (Lindeman, 1942; Pimm, 1982). Both are fundamental aspects of biological systems that describe how resources are used and energy is transferred among organisms (Paine, 1980), and thereby also how communities of living organisms are linked to their abiotic environment (Begon, 2006). On the one hand, organisms rely on their resources but conversely also exert strong predation pressure on resource populations. These so called ‘bottom-up’ and ‘top-down’ effects can incite strong direct and indirect effects throughout ecosystems (Wootton, 1994; Terborgh et al., 2001; Worm et al., 2002; Knight et al., 2005; Montoya et al., 2009). Indirect effects can arise, for example, when predators reduce the abundance of their prey, and thereby indirectly relax the consumption on

lower trophic levels. These indirect effects that, for example, predators exert on plants via herbivores are so called trophic cascades (Pace et al., 1999; Shurin et al., 2002). Trophic cascades can also follow perturbations to species at lower or higher trophic levels (Wootton, 1994). Let me illustrate this with one very simple example, a three-level food chain from the Pacific coast. In this system, a sea otter feeds on sea urchins, that in turn feed on kelp (Estes and Palmisano, 1974; Estes et al., 2010). In the simplest case, the sea otter will constrain the sea urchin population to low levels. If taken one step further, by controlling the abundance of sea urchins, the sea otter indirectly causes a positive effect on kelp by alleviating it from the top down pressure. Whereas decreases in the sea otter population, whether historically due to hunting or more recently due to climate change, resulted in an increase in the sea urchin population. As sea urchins graze on kelp, this led to less kelp cover, which consequently also affected fish populations that use the kelp forest as habitat (Estes and Palmisano, 1974; Estes et al., 2010). This is a very prominent example for a top-down driven trophic cascade in which the loss of a keystone predator, the sea otter, will affect most species of an ecosystem (Paine, 1966; Estes and Palmisano, 1974). Cascading trophic interactions are (almost) ubiquitous in nature (Schmitz et al., 2000; Shurin et al., 2002) and have also been shown to cause reverberating effects across ecosystem boundaries (see, for example, Knight et al., 2005). Furthermore, they have found broad (ecological) applications including the management of herbivorous pest species in agricultural systems (see, for example, Liere et al., 2015), and can also be translated to broader levels of biological organization, such as the community level (Hairston et al., 1960; Oksanen et al., 1981; Borer et al., 2005; Otto et al., 2008).

In reality, ecosystems contain unknown numbers of organisms, and thus trophic interactions are much more complex, surpassing by far the simplicity of food chains and trophic cascades (Williams and Martinez, 2000; Dunne, 2005; Jacob et al., 2011; Thompson et al., 2012; Brose et al., 2019). This means (local) biodiversity is organized into (non-random) ecological networks of interacting species, like food webs. Food webs are the backbone upon which biomass flows through local ecosystems (Yodzis and Innes, 1992; Brose et al., 2006a; Delmas et al., 2019), and as such are a central organizing theme in nature (Elton, 1927; Dunne, 2005). They have been intensively studied, both empirically and theoretically (see the review by Layman et al., 2015 for an overview). In food webs species are closely interlinked; on the one hand, through direct (pair-wise) interactions, for example, predation and competition, but also through indirect interactions like the outlined trophic cascades. Such indirect interactions are an important source of complexity in natural communities (Wootton, 1994; Abrams et al., 1996; Montoya et al., 2009), and in food webs, they can also include apparent competition, predator-mediated coexistence, exploitative competition and indirect mutualism (Wootton, 1994; Morin, 1999). Given

the entangled structure of food webs, perturbations like the loss of a species can trigger extinctions of other dependent species, and set in motion a cascade of secondary extinctions. This extinction cascade can snowball through the entire network, alter the community composition and network structure, and in the worst case drastically reduce the number of species and trophic complexity (Ebenman and Jonsson, 2005; Eklöf and Ebenman, 2006; Dunne and Williams, 2009; Curtsdotter et al., 2011; Riede et al., 2011; Eklöf et al., 2012). The complex ways in which species interact in food webs is, in part however, also the reason why predicting their responses to environmental impacts like the loss or fragmentation of habitat (e.g., due to human land use changes) but also biological invasions, is very difficult and demands approaches that can account for this complexity. One approach providing this are theoretical models of food webs that combine mathematics and ecology. More specifically, they simplify the complex ecological processes that play out in food webs on the basis of mathematical concepts (see, for example, Yodzis and Innes, 1992; Brose et al., 2006a; Allesina et al., 2008; Dunne and Williams, 2009; Curtsdotter et al., 2011; Eklöf et al., 2013). This simplification facilitates the study of isolated mechanisms but can also scale up ecological processes to real-world complexity.

2.2 Theoretical models of food webs

Theoretical models of food webs typically present food webs, and ecological networks in general, by a (directed) graph with nodes representing species and edges representing interactions between species (often with weights such as rates or capacity, for example feeding links with interaction strengths) (Dunne, 2005; Dale and Fortin, 2010; Delmas et al., 2019). This representation provides an useful abstraction of complex ecological systems by summarizing their information within a single graph object (Dale and Fortin, 2010; Delmas et al., 2019). Two types of theoretical models of food webs are the methodological backbone of this thesis: dynamical food web models (research chapters 1 and 3) and Bayesian network representations of food webs (research chapter 2).

Dynamical models Dynamical models of food webs track the flow of energy stored in plant and animal biomass trough (local) ecosystems by explicitly simulating population dynamics (see, for example, Berlow et al., 2009; Binzer et al., 2011; Curtsdotter et al., 2011; Schneider et al., 2016). These models are thus also referred to as bioenergetic models, defining plant species growth as energy uptake from nutrients, feeding as biomass transfer from one population into another, and metabolism

as conversion of energy into thermal energy (Yodzis and Innes, 1992; Williams and Martinez, 2000). In its very general form, the change in population abundance (biomass B_i) of species i over time reads as

$$\frac{dB_i}{dt} = r_i B_i - \sum_j (B_i B_j f_{ji}) + \sum_k (B_k B_i f_{ki}) e - x_i B_i \tag{I.1}$$

This equations describes the summed feeding on species i by all its predators j, by a rate f_{ji}, and the summed feeding of species i on all its prey species k, by a rate f_{ki}. The assimilation efficiency e_i defines how much of one unit of consumed prey biomass can be converted into species i's biomass, while the growth rate r_i and the metabolic rate x_i define species i's intrinsic biomass gains and losses. Starting with initial biomass densities, the changes of the species over time can be integrated using a system of coupled ordinary differential equations. This general version of the model can be scaled up to complex food webs comprising of many species and even more feeding links. By accounting for both direct and indirect interactions, dynamical models offer a highly detailed description of (multi-)trophic communities (Berlow et al., 2009; Binzer et al., 2011; Curtsdotter et al., 2011; Riede et al., 2011), and, for example, can unravel how the structure of food webs is involved in many key ecosystem properties (e.g., persistence and stability (Delmas et al., 2017), or ecosystem functioning (Schneider et al., 2016)). Studies that made use of dynamical models to explore ecological impacts of global change in food webs are for example, Romanuk et al. (2009) and Binzer et al. (2012, 2016). However, their full potential is only realized if all model parameters are realistically represented.

One way to achieve this is to derive model parameters, for example, for metabolism and feeding, from the body mass of interacting species (Brose et al., 2006a; Otto et al., 2007; Berlow et al., 2009; Schneider et al., 2012; Schneider et al., 2016). Body mass can explain many ecological processes and patterns (Peters, 1983; Jonsson et al., 2005; Brose et al., 2006a; Otto et al., 2007; Riede et al., 2011), and has been found to constitute a 'super trait' that determines many other species traits, including physiological rates like metabolism, growth, reproduction (Brown et al., 2004; Savage et al., 2004), interaction strengths with coexisting species (Petchey et al., 2008; Rall et al., 2012), as well as behavioral characteristics (Dial et al., 2008) and movement (Hirt et al., 2017a; Hirt et al., 2018). The use of body mass as the sole trait characterizing a species, determining its other relevant features as well as the underlying metabolic principles (Woodward et al., 2005), has greatly simplified model parameterization (Hudson and Reuman, 2013; Jonsson et al., 2018). Consequently, much of current food web theory is built on body mass determined predator-prey interactions that drive community dynamics (Yodzis and Innes, 1992; Woodward et al., 2005; Brose et al., 2006a,b; Brose, 2010; Brose et al., 2019). One recent example for a dynamic model that is built on allometric principles for metabolism,

growth and feeding is the allometric trophic network model described in Schneider et al. (2016), which the authors made use of to predict links between community composition (animal diversity) and ecosystem functioning driven by trophic interactions.

Bayesian network models Another approach to model food webs is based on Bayesian networks, or Belief networks. The use of Bayesian networks for representing food webs has been proposed by Eklöf et al. (2013) as a means to study secondary extinctions in (local) food webs. Bayesian networks simply are a collection of random variables determining the presence or absence of species, with arrows describing their conditional dependencies. In the context of food webs, this means their feeding relationships (Jensen, 1996; Eklöf et al., 2013). Therefore, the probability $P(\neg C|f)$ of a species C going extinct can be expressed as a function of the fraction f of its resources that are absent:

$$P(\neg C|f) = \pi_C + (1 - \pi_C)B(f) \tag{I.2}$$

In this equation, π_C defines species C's baseline extinction probability (the likelihood of extinction despite all its resources being present), and $B(f)$ defines a monotonically increasing function of f such that $B(0) = 0$ and $B(1) = 1$. This representation allows species' extinction probabilities to increase gradually with resource loss, and also quantifies the probability of species going extinct for causes other than those represented by the network (i.e., lets them be nonzero even when species have full access to their resources; in contrast to simple topological models like Dunne and Williams (2009)). In a Bayesian network representation of a food web, one determines the extinction probabilities of all species in a food web via a bottom-up calculation process: this means, one starts with basal species, then moves on to species only consuming those basal species, and so on, until the highest trophic level is reached. For this reason, the Bayesian network approach requires food webs that are acyclic as otherwise this bottom-up approach would not work, and in this representation cannot capture top-down effects since predators are influenced by their prey whereas the prey dynamics do not depend on the presence of their predators at all.

3 | Aspects of spatial scale

3.1 Food webs in a metacommunity context

The predictions derived from such non-spatial food web models are crucial for understanding how species extinctions reverberate through food webs and how this affects food web persistence and stability. However, by neglecting aspects of spatial scale, these studies also ignore the potentially

strong impact that spatial aspects can have on (local) communities (Gibert and Yeakel, 2019). It is well established that fluxes of organisms across habitat or even ecosystem boundaries can have major consequences for (local) community dynamics (Polis et al., 1997; Knight et al., 2005; Gibert and Yeakel, 2019) and that food webs comprise of organisms that live in spatially heterogeneous and changing landscapes (Polis et al., 1997). Nevertheless, studies of food webs and trophic cascades majorly focus on feeding interactions between species within a certain habitat (see, for example, Terborgh et al., 2001; Worm et al., 2002; Schneider et al., 2016, but see also Holt, 2002; Melián and Bascompte, 2002; Knight et al., 2005; Amarasekare, 2008). However, even if local food webs may appear discrete, they are open and connected in multiple ways to outside influences (Polis et al., 1997; Holt, 2002; Holt and Hoopes, 2005; Amarasekare, 2008), for instance, by varying amounts of emigration and immigration. Therefore, conceptualizing food webs as community assemblages within a particular habitat neglects the strong impact that spatial aspects can have on food web structure, dynamics and stability (see, e.g., Pillai et al., 2011; Gravel et al., 2011a). For example, Gravel et al. (2011a) demonstrated that regional dynamics can enhance the stability of food webs that were locally prone to extinction, and Knight et al. (2005) could show that local feeding interactions within one habitat can also cause reverberating effects across ecosystem boundaries (in their study system, fish indirectly facilitated terrestrial plant reproduction through cascading trophic interactions across ecosystem boundaries). Consequently, studies addressing food webs as spatially isolated systems very likely miss important ecological patterns and processes that emerge at scales outside the local habitat. Among these are, for example, spatial rescue effects, the co-distribution of predators and their prey, species range limits, and the restructuring of food webs considering different spatial scales (see the review by Guzman et al., 2018). The study of these spatial patterns and processes is the core of metapopulation and metacommunity research (Hanski, 1998; Hanski and Ovaskainen, 2000; Leibold et al., 2004; Holyoak et al., 2005), which primarily focus on the interactions of subpopulations or respectively subcommunities through the dispersal of organisms. Thereby, they generally ignore interactions between species within local habitat patches, especially complex interactions that scale up to ecological networks like food webs (see the review by Guzman et al., 2018 and references therein). In summary, this means food web research typically disregards space, whereas studies incorporating space usually disregard species interactions.

Two decades ago, food web ecology began to study aspects of spatial scale, mostly based on classical metapopulation theory (Levins, 1969; Hanski, 1998), and recently the number of advances has been increasing (see, for example, Pillai and Gonzalez, 2010; Pillai et al., 2011; Gravel et al., 2011a; Liao et al., 2016, 2017a,b,c; McWilliams et al., 2019, and reviews by Holt, 2002; Amarasekare, 2008;

Hagen et al., 2012). Systematic explorations, however, are scarce (Gonzalez et al., 2011; McWilliams et al., 2019) and for realistically complex food webs virtually absent, as most previous studies have been restricted to small systems like trophic chains or simple food web motifs and/or small landscapes and/or assumed implicit space (e.g., Melián and Bascompte, 2002; McCann et al., 2005; Calcagno et al., 2011; Gravel et al., 2011a; Pillai et al., 2011; Liao et al., 2016, 2017a). These small-scale and/or spatially-implicit approaches consistently demonstrated the importance of considering spatial scale in food webs, yet, despite their important contributions, they leave a large gap between the current modeling approaches and the complexity of natural ecosystems in predicting consequences of spatial changes for species, food webs, and biodiversity. Therefore, approaches are in need that can advance our mechanistic understanding of how trophic interactions and dispersal processes mediate complex community responses to environmental changes such as habitat destruction. In this thesis, I address this challenge by analyzing food webs in a metacommunity context (i.e., meta-food-webs or multitrophic metacommunities). This allows me to elucidate what drives species persistence and community assembly in trophically complex food webs in fragmented landscapes, and further to delve into the mechanisms that drive food web responses to global changes at different levels of biological organization and spatial scales. I specifically seek to identify variations in species extinction rates across trophic levels and to associate these variations with environmental factors. Detecting this will yield important insights into the underlying changes in ecosystem stability under global change and their robustness to extinction and invasion (see, for example, Tylianakis et al., 2007; Tylianakis et al., 2008; Tylianakis and Binzer, 2014).

3.2 The role of dispersal in fragmented landscapes

Human land use is fragmenting landscapes (Haddad et al., 2015) and in such increasingly fragmented and patchy landscapes, species persistence critically depends on dispersal (Hanski, 1998; Hanski and Ovaskainen, 2003; Grilli et al., 2015). This means, as long as organisms can disperse between habitat patches and thus recolonize empty ones (so called spatial rescue effects), species can persist at the metapopulation or metacommunity level, even though local populations might undergo extinction (Levins, 1969; Hanski, 1998; Hanski and Ovaskainen, 2003; Leibold et al., 2004; Holyoak et al., 2005; Grilli et al., 2015). Therefore, the dispersal ability of species is an important driver of community dynamics, determining the rate of species immigration into habitat patches (Loreau and Mouquet, 1999) as well as the mixing or the spatial segregation among species (Pacala and Levin, 1997). Fragmented landscapes, however, can greatly vary in their quality and productivity, differ in resource abundance and consumer behavior as well as landscape connectivity, reaching from almost total isolation to highly

connected. All these factors influence the exchange rates among habitats and thus can have significant implications for (local) food web dynamics (see the review by Polis et al., 1997 and references therein). Therefore, in their review, Polis et al. (1997) propose an integration of landscape and food web ecology to address the importance of spatial flows among habitats for local food web dynamics. This flow rate between habitats (or habitat fragments) depends on various environmental but also organismal factors. For example, the spatial configuration of habitat, the distance between habitats, as well as habitat geometry and area, but also the mobility of organisms (i.e., their movement capacities and dispersal abilities) (Polis et al., 1997; Thompson and Gonzalez, 2017; Hirt et al., 2018). All these factors determine which habitat patches compose the spatial network of a species, implying that every species potentially experiences its own version of the landscape, depending on which habitat patches it can connect (Olesen et al., 2010; Hirt et al., 2018). This applies especially to food webs in which species are distributed over multiple trophic levels and thus also differ in their habitat requirements and dispersal abilities. This species-specific version of the landscape depends, for example, on a species' dispersal range, movement capacity and movement mode (Jenkins et al., 2007; Hirt et al., 2018). However, land use changes often decrease the suitability of the habitat matrix. This can heighten the stress and mortality during dispersal, and thereby, drastically reduce dispersal and colonization success (Franklin and Lindenmayer, 2009). Therefore, even though dispersal has been shown to be beneficial or often even crucial for population and community persistence in heavily fragmented landscapes, there are also risks and losses associated with it (Bonte et al., 2012). Additionally, other influences on movement capacity and dispersal patterns (e.g., due to climatic changes (O'Connor et al., 2007; Eklöf et al., 2012; Årevall et al., 2018)) could alter the likelihood of species persistence.

4 | Research objectives and study outline

4.1 Research objectives

Human-induced global change, and foremost land use changes, are responsible for the current biodiversity crisis. As these changes will continue to increase in the future, we must be able to understand the ecological impacts of global change on complex communities like food webs. What happens when the balance in a food web is disturbed and why are some species more likely to go extinct than others? Answering these questions requires a good mechanistic understanding of the underlying ecological processes, like species interactions and dispersal, that determine food web responses to global change impacts and their correlations with landscape properties, for instance, the spatial configuration of habitat (i.e, landscape structure). Knowledge of the relative importance

of these local and spatial processes and their biological implications in terms of the underlying mechanisms is crucial for assessing why some species are more sensitive to environmental changes, what determines this variability and thus shapes the species diversity patterns we observe. Despite the relevance of this topic, while scanning the scientific literature, I became aware that how food webs respond to global changes across habitat boundaries, such as the loss and fragmentation of habitat or biological invasions, is only poorly understood. As follows from the previous sections, this is, in part, because to date, food web ecology for the most part considers food webs at the level of local ecosystems, and systematic explorations incorporating aspects of spatial scale are scarce.

In this thesis, I address this scientific gap by bridging two core groups of ecology—food web and metacommunity ecology. More specifically, I integrate complex food webs and spatially-explicit patch networks linked by dispersal into meta-food-webs (or multitrophic metacommunities). By analyzing food webs in a metacommunity context, I incorporate for the first time real-world complexity for local and spatial processes which allows me to elucidate food web responses to global change across habitat boundaries. My primary aim thereby is to investigate how land use changes and biological invasions affect species persistence and community assembly in meta-food-webs, and to unravel the underlying mechanisms that are responsible for species extinctions and that shape the emerging species diversity patterns.

To approach these aims, I propose new theoretical frameworks for studying meta-food-webs that enable me firstly, to delve into the underlying mechanisms governing the impacts of global change on food webs in complex landscapes, and secondly, to explore variations in these responses among species, trophic groups, and landscapes. These frameworks are built on the food web models outlined in section 2.2 and make it possible to explore if and how the interplay of species interactions, dispersal and landscape properties mediate food web responses to global changes.

4.2 Study outline

In research chapter 1, I test to what extent trophic interactions and dispersal dynamics influence the persistence of species in meta-food-webs when landscapes become increasingly fragmented. I focus specifically on identifying species or trophic groups that have elevated extinction risks which then may result in a reorganization of the meta-food-web. I do so by merging bioenergetic dynamic food web models (Schneider et al., 2016) and spatial network models (Hirt et al., 2018) that use allometric scaling relationships of trophic and spatial processes as a unifying principle into a meta-food-web model. This means both models employ body mass a super trait that fully characterizes each species, yielding a model that follows allometric scaling laws for metabolism, growth, feeding

and dispersal. By explicitly modelling the local population dynamics between species and the spatial dispersal dynamics between local populations, this method can account for both the direct and indirect effects arising from these processes, offering a highly detailed description of trophic communities. Thereby, this framework allows me to delve into the underlying ecological mechanisms (i.e., trophic interactions and dispersal dynamics) that determine species persistence and community assembly in multitrophic communities consisting of 30 animal and 10 plant species in increasingly fragmented landscapes. Specifically, I assess the effect of fragmentation on the emerging species diversity patterns by analyzing how the number of habitat patches and their degree of isolation affect local and regional diversity and community composition. I find habitat isolation to be the key driver for species loss and diversity decline with the most detrimental impacts on large-bodied top predators despite their superior dispersal abilities and thus higher landscape connectivity. I attribute this elevated extinction risk of top species to bottom-up energy limitations arising in highly isolated landscapes.

Building on the establishment that food web responses to habitat fragmentation are mediated by feeding and dispersal dynamics, deconstructing meta-food-webs from top to bottom, in research chapter 2, I test the effects of progressive habitat loss. To test this, I combine classic metapopulation models on fragmented landscapes (Hanski and Ovaskainen, 2003; Grilli et al., 2015), with a Bayesian network representation of food webs for calculating local species' extinction rates (Eklöf et al., 2013). This method enables me to explore variations in species extinction rates in large multitrophic metacommunities with hundreds of species and patches that undergo different scenarios of progressive habitat loss. In addition to random habitat loss, I either prioritize the removal of valuable or non-valuable patches by ranking patches with respect to their importance to the persistence of the metacommunity as a whole. I further demonstrate that this method can be readily applied to empirical systems using the the plant-mammal Serengeti food web dataset (Baskerville et al., 2011), an iconic but highly threatened system, as a case study. The results show that metacommunity persistence strongly depends on the order of habitat removal: Removing the least valuable patches first, often let the metacommunities withstand the removal of more than 90% of their patches; whereas, focusing on removing the most valuable patches first but also random patch removal, very quickly resulted in a collapse of metacommunities. In all cases, I find that species' vulnerability to habitat loss is greater at higher trophic levels, a pattern which is (mostly) independent of model parameterization, emphasizing the generality of these trends. This also holds true for the patterns I find for the plant-mammal Serengeti food web dataset.

In addition to how land use changes alter species extinction rates in multitrophic metacommunities at different levels of biological organization and spatial scales, I set out to investigate what facilitates

or prevents biological invasions in meta-food-webs. Therefore, in research chapter 3, I test under which circumstances invasive alien species can successfully invade meta-food-webs (i.e., establish a stable population and spread through the new environment). I test this by developing a holistic network-based approach that simulates single-species invasions by animal and plant species in landscapes varying in their landscape structure (i.e., clustered and random distribution of habitat) and environmental conditions (i.e., levels of nutrient supply). In doing so I explore which underlying ecological mechanisms facilitate or prevent biological invasions in meta-food-webs and to what extent invasion success depends on invasive species traits and meta-food-web structures. I find that knowledge of the landscape structure is crucial to accurately predict biological invasions and in particular how successful an invader can spread across a new environment, provided there is sufficient nutrient supply in the landscape. The latter is most applicable to species at higher trophic positions whose persistence relies on sufficient amounts of resources in the landscape. Good dispersal abilities promote the spread of invasive species, thereby, showing that invasion success is determined by the combination of abiotic (i.e., landscape structure and environmental conditions) and biotic factors (i.e., species interactions and dispersal).

Overall, this thesis studies the underlying ecological mechanisms that mediate food web responses to global changes by combining real-world complexity of two key ecological processes: feeding and dispersal. Thereby, this thesis advances the mechanistic understanding of how complex food webs respond to global changes and in general, elucidates the collective dynamics in complex ecological networks that span across habitat boundaries. The research chapters outlined above and presented in detail in the following part of this thesis provide novel and important insights for community ecology and conservation that would not have been revealed without this analyses of complex communities at different levels of biological organization and spatial scales.

II

Research Chapters

1 | Research Chapter 1

The biggest losers: habitat isolation deconstructs complex food webs from top to bottom

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The biggest losers: habitat isolation deconstructs complex food webs from top to bottom

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Habitat fragmentation threatens global biodiversity. To date, there is only limited understanding of how the different aspects of habitat fragmentation (habitat loss, number of fragments and isolation) affect species diversity within complex ecological networks such as food webs. Here, we present a dynamic and spatially explicit food web model which integrates complex food web dynamics at the local scale and species-specific dispersal dynamics at the landscape scale, allowing us to study the interplay of local and spatial processes in metacommunities. We here explore how the number of habitat patches, i.e. the number of fragments, and an increase of habitat isolation affect the species diversity patterns of complex food webs (α-, β-, γ-diversities). We specifically test whether there is a trophic dependency in the effect of these two factors on species diversity. In our model, habitat isolation is the main driver causing species loss and diversity decline. Our results emphasize that large-bodied consumer species at high trophic positions go extinct faster than smaller species at lower trophic levels, despite being superior dispersers that connect fragmented landscapes better. We attribute the loss of top species to a combined effect of higher biomass loss during dispersal with increasing habitat isolation in general, and the associated energy limitation in highly fragmented landscapes, preventing higher trophic levels to persist. To maintain trophic-complex and species-rich communities calls for effective conservation planning which considers the interdependence of trophic and spatial dynamics as well as the spatial context of a landscape and its energy availability.

1. Introduction

Understanding the impact of habitat fragmentation (habitat loss, number of fragments and isolation) on biodiversity is crucial for ecology and conservation biology [1–3]. A general observation and prediction is that large-bodied predators at high trophic levels which depend on sufficient food supplied by lower trophic levels are most sensitive to fragmentation, and thus, might respond more strongly than species at lower trophic levels [4,5]. However, most conclusions regarding the effect of fragmentation are based on single species or competitively interacting species (see references within [6–8], but see for example [9–11] for food chains and simple food web motifs). There is thus limited understanding how species embedded in complex food webs with multiple trophic levels respond to habitat fragmentation [4,12–15], even though these networks are a central organizing theme in nature [16,17].

The stability of complex food webs is, among others, determined by the number and strength of trophic interactions [18]. While it is broadly recognized that habitat fragmentation can have substantial impacts on such feeding relationships [19,20],

we lack a comprehensive and mechanistic understanding of how the disruption or loss of these interactions will affect species persistence and food web stability [15,19,21,22]. Assuming that a loss of habitat, a decreasing number of fragments, and increasing isolation of the remaining fragments disrupt or weaken trophic interactions [7], thereby causing species extinctions [15,20], population and community dynamics might change in unexpected and unpredictable ways. This change in community dynamics might lead to secondary extinctions which potentially cascade through the food web [23,24].

Habitat loss, i.e. the decrease of total habitable area in the landscape or a reduction in patch size, can limit population sizes and biomass production, which might drive energy-limited species extinct [25,26] and subsequently entail cascading extinctions [23]. Successful dispersal among habitat patches might prevent local extinctions (spatial rescue effects), and thus, ensure species persistence at the landscape scale [27,28]. Whether dispersal is successful or not depends, among other factors, on the distance an organism has to travel to reach the next habitat patch and on the quality of the matrix the habitat patches are embedded in (in short: the habitat matrix) [29]. With progressing habitat fragmentation, suitable habitat becomes scarce and the remaining habitat fragments increasingly isolated [3,30], affecting the dispersal network of a species. As a consequence, organisms have to disperse over longer distances to connect habitat patches, which in turn might increase dispersal mortality and thus promote species extinctions [2]. Also, habitat fragmentation often increases the hostility of the habitat matrix, e.g. owing to human land use and landscape degeneration [3,31,32]. The increased matrix hostility might further reduce the likelihood of successful dispersal between habitat patches as the movement through a hostile habitat matrix is energy intensive, and thus, population biomass is lost [29,31]. This loss depends on the distance an organism has to travel and its dispersal ability, i.e. its dispersal range and the energy it can invest into movement. Finally, the detrimental effects of habitat loss and increasing isolation are likely to interact, as dispersal mortality can be expected to have a larger *per capita* effect when a population is already declining owing to decreasing habitat.

In this context, superior dispersers might have an advantage over species with restricted dispersal abilities if the distances between habitat patches expand to a point where dispersal-limited species can no longer connect habitat patches. If this is the case, increasing habitat isolation impedes the ability of organisms to move across a fragmented landscape and prevents spatial rescue effects buffering against local extinctions. Increasing habitat isolation might result in increased extinction rates and ultimately lead to the loss of dispersal-limited species from the regional species pool. As large animal species are, at least up to a certain threshold, faster than smaller ones [33,34], they should also be able to disperse over longer distances [4,35,36]. In fragmented landscapes, this body mass-dependent scaling of dispersal range might favour large-bodied consumers such as top predators, and thus, increase top-down pressure resulting in top-down regulated communities.

Empirical evidence and results from previous modelling approaches, however, suggest that species at higher trophic positions are most sensitive to isolation [9,15,37–39]. Modelling tri-trophic food chains in a patch-dynamic framework, Liao *et al.* [9,10], for example, show that increasing habitat fragmentation leads to faster extinctions of species at higher trophic levels, which they ascribe to reduced availability of prey [9]. In the fragmentation experiment by Davies *et al.* [39], on the other hand, the observed loss of top species is attributed to the unstable population dynamics of top species under environmental change.

Despite its relevance, a realistic picture and comprehensive understanding of how natural food webs might respond to different aspects of fragmentation such as habitat loss or increasing isolation, and any alteration to the spatial configuration of habitat in general, are lacking. To understand how fragmentation affects the diversity of communities organized in complex food webs requires knowledge of the interplay between their local (trophic) and spatial (dispersal) dynamics. The latter are determined by the number of fragments in the landscape and the distance between them, which can potentially affect the local trophic dynamics. We address this issue using a novel modelling approach which integrates local population dynamics of complex food webs and species-specific dispersal dynamics at the landscape scale (which we hereafter refer to as the meta-food-web model, see figure 1 for a conceptual illustration). Our spatially explicit dynamic meta-food-web model allows us to explore how direct and indirect interactions between species in complex food webs together with spatial processes that connect sub-populations in different habitat patches interact to produce diversity patterns across increasingly fragmented landscapes. Specifically, we ask how the number of fragments and increasing habitat isolation impact the diversity patterns in complex food webs. We further ask which species or trophic groups shape these patterns.

Following general observations and predictions, we expect species diversity within complex food webs to decrease along a gradient of isolation. Based on the substantial variation in both dispersal abilities and energy requirements among species and across trophic levels [4,25,39], we expect species at different trophic levels to strongly vary in their response to isolation. Specifically, we expect certain trophic groups such as consumer species at lower trophic ranks with limited dispersal abilities or top predators with strong resource constraints to be particularly sensitive to isolation. Additionally, with a larger number of fragments we expect more potential for rescue effects, thus fostering survival. This might especially apply to species with large dispersal ranges, which allow them to connect many habitat patches. We test our expectations using Whittaker's classical approach of α-, β- and γ-diversity [40], where α- and γ-diversity describe species richness at the local (patch) and regional (metacommunity) scale, respectively, and β-diversity accounts for compositional differences between local communities.

2. Methods

In the following, we outline a methods summary, for detailed information on equations and parameters see the methods section in the electronic supplementary material. We consider a multitrophic metacommunity consisting of 40 species on a varying number of randomly positioned habitat patches (the meta-food-web, figure 1*b*). All patches have the same abiotic conditions and each patch can potentially harbour the full food web, consisting of 10 basal plant and 30 animal consumer species. The potential feeding links (i.e. who eats whom) are constant over all patches (figure 1*a*,*b*) and are as well as the feeding dynamics determined by the allometric food web model by Schneider *et al.* [41]. We use a dynamic bioenergetic model formulated in terms of ordinary differential equations that describe the feeding and dispersal dynamics. The rate of change in biomass density of a species depends on its biomass gain by feeding and immigration and its biomass loss by

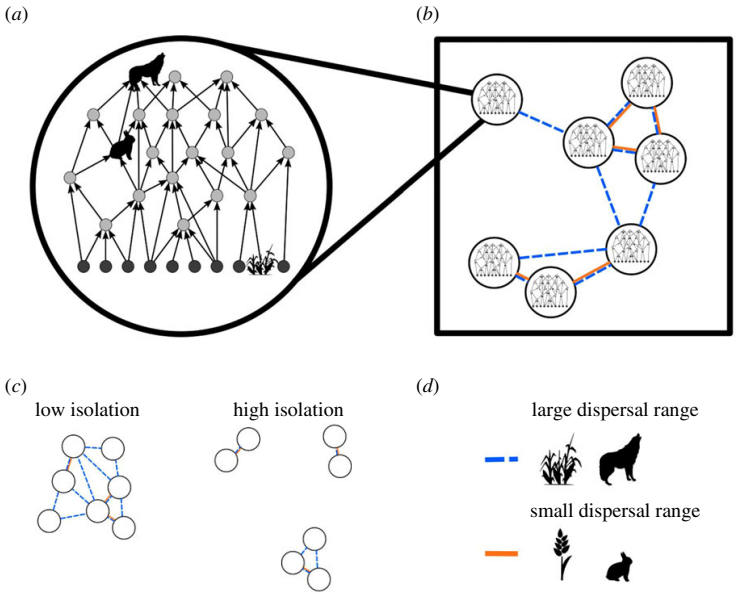

Figure 1. Conceptual illustration of our modelling framework. In our meta-food-web model (*b*), we link local food web dynamics at the patch level (*a*) through dynamic and species-specific dispersal at the landscape scale (*d*). We consider landscapes with identical but randomly distributed habitat patches, i.e. all patches have the same abiotic conditions, and each patch can potentially harbour the full food web. We model fragmented landscapes which differ in the number of habitat patches and the mean distance between patches (*c*).

metabolism, being preyed upon and emigration. We integrate dispersal as species-specific biomass flow between habitat patches (figure 1*b*,*d*). Based on empirical observations (e.g. [35]) and previous theoretical frameworks (e.g. [4,12,34,42]), we assume that the maximum dispersal distance of animal species increases with their body mass. As plants are passive dispersers, we model their maximum dispersal distance as random and body mass independent. We model emigration rates as a function of each species' *per capita* net growth rate, which is summarizing local conditions such as resource availability, predation pressure, and inter- and intraspecific competition [43]. During dispersal, distance-dependent mortality occurs, i.e. the further two patches are apart, the more biomass is lost to the hostile matrix separating them. We constructed 30 model food webs and simulated each food web on 72 different landscapes. For each simulation, we generated landscapes on two independent gradients covering two aspects of fragmentation, namely number of patches and habitat isolation (figure 1*c*). We achieved a full range for the gradient of habitat isolation (landscape connectance ranging from 0 to 1, figure 3*c*). Additionally, we performed dedicated simulation runs to reference the two extreme cases, i.e. (i) landscapes in which all patches are direct neighbours without a hostile matrix, and thus, no dispersal mortality and (ii) fully isolated landscapes, in which no species can bridge between patches, and thus, a dispersal mortality of 100%. Additionally, we tested a null model in which all species have the same maximum dispersal distance. To visualize the impact of number of patches and habitat isolation on species diversity, we used generalized additive mixed models from the mgcv package in R [44,45]. See the electronic supplementary material for detailed information on the maximum dispersal distance, the additional simulations and the statistical analysis.

3. Results

(a) Species diversity patterns

Our simulation results identify habitat isolation (defined as the mean distance between habitat patches, $\overline{\tau}$, figure 2, *x*-axis) as the key factor driving species diversity loss. As expected, we find fewer species on patches (the averaged local diversity, $\overline{\alpha}$) in landscapes in which habitats are highly isolated (figure 2*a*). In contrast to the decrease in $\overline{\alpha}$-diversity, β-diversity (figure 2*b*), which describes differences in the community composition between patches, increases with habitat isolation. This increase starts around the inflection point of the landscape connectance at a mean patch distance of $\log_{10}\overline{\tau} \approx$ of -0.5, at which 50% of all possible patch to patch connections are lost (figure 3*c* and the electronic supplementary material, figure S4). γ-diversity, the species diversity in the landscape, shows a more complicated pattern. First it decreases owing to the loss of $\overline{\alpha}$-diversity with habitat isolation. This decrease is then reversed by the increase of β-diversity and the γ-diversity increases again with habitat isolation (figure 2*c*). The number of habitat patches in a landscape, Z (figure 2, *y*-axis), only marginally affects the diversity patterns. The additional simulations of the two extreme cases (i.e. joint scenario with no dispersal loss and fully isolated scenario with 100% dispersal mortality) support these patterns (see the electronic supplementary material, section S7 for the corresponding results). We further show that the isolation-induced species loss also translates into a loss of trophic complexity, i.e. isolated landscapes are characterized by reduced food webs with fewer species and fewer trophic levels (see the electronic supplementary material, figure S2).

(b) Differences among trophic levels

As the number of patches only marginally affects the species diversity patterns, we hereafter focus on the effects of habitat isolation on trophic-dependent differences among species (figure 3). In figure 3, biomass densities, B_i, and landscape connectances, ρ_i, represent the average of each species i over all food webs. Species are ranked according to their body

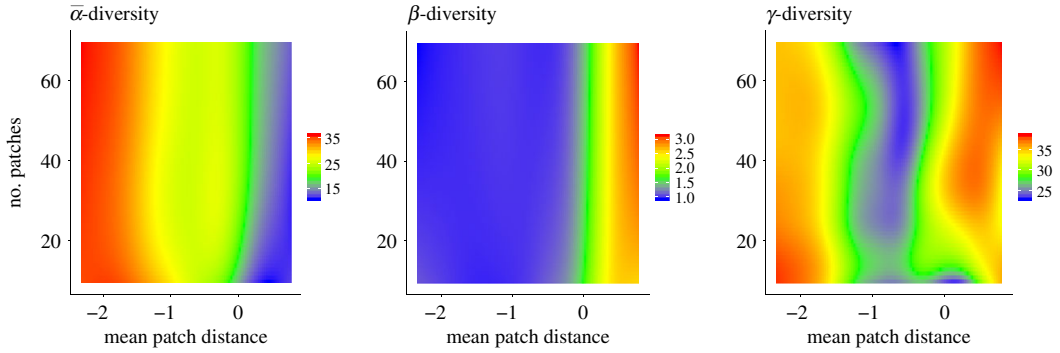

Figure 2. Heatmaps visualizing $\overline{\alpha}$-, β- and γ-diversity (colour-coded; *z*-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; *x*-axis) and the number of habitat patches (*Z*; *y*-axis), respectively. We generated the heatmaps based on the statistical model predictions (see the electronic supplementary material).

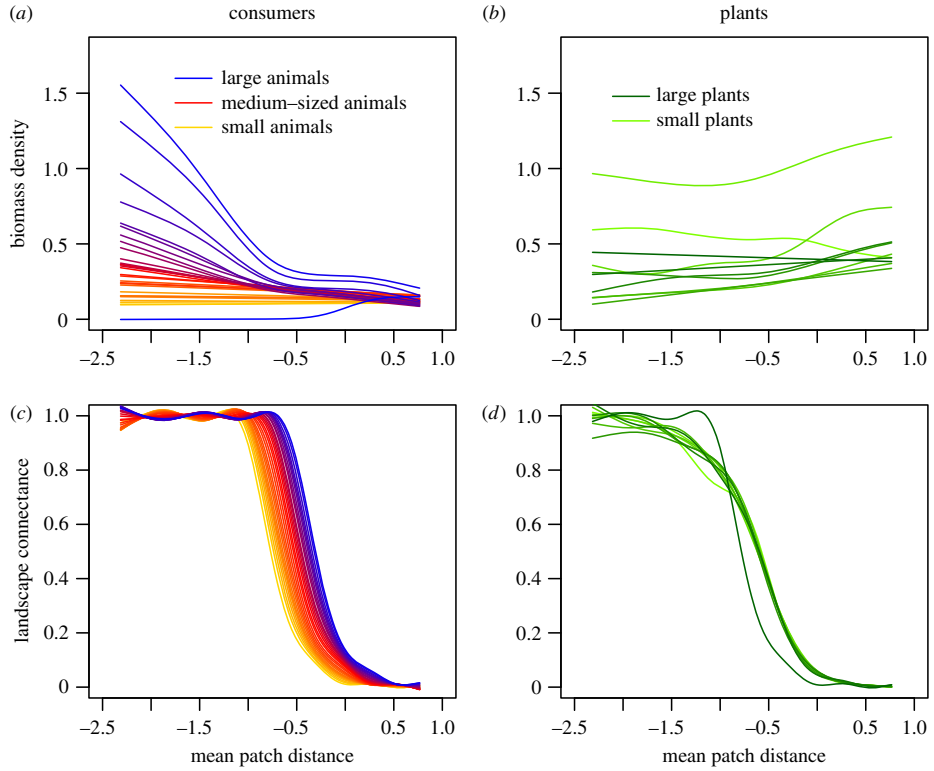

Figure 3. Top row: Mean biomass densities [$\log_{10}$(biomass density + 1)] of animal consumer species (*a*) and basal plant species (*b*) over all food webs (B_i, $\log_{10}$-transformed; *y*-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; *x*-axis). Each colour depicts the biomass density of species *i* averaged over all food webs: (*a*) colour gradient where orange represents the smallest, red the intermediate and blue the largest consumer species; (*b*) colour gradient where light green represents the smallest and dark green the largest plant species. Bottom row: Mean species-specific landscape connectance (ρ_i; *y*-axis) for consumer (*c*) and plant species (*d*) over all food webs as a function of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; *x*-axis). See the electronic supplementary material, figure S9 for standard errors in biomass densities for four exemplary species.

mass. Thus, although species body masses differ between food webs, species 1 is always the smallest, species 2 the second smallest and so forth. The same applies to ρ_i, where the landscape connectance of consumer species is body mass dependent, but the connectance of plant species is body mass independent (see the methods section). In well-connected landscapes (i.e. landscapes with small mean patch distances, $\overline{\tau}$), large and medium-sized consumer species (except the very largest) have higher population biomass densities than smaller consumers (figure 3*a*,*c*). With expanding distances between habitat patches, large-bodied consumers at high trophic positions (figure 3*a*, red to blue lines) show a particularly strong decrease in population biomass densities. Small consumer species (figure 3*a*, orange lines) are generally less affected by increasing habitat isolation. Plant species show a less consistent response to increased isolation, with most

species slightly increasing their biomass density (figure 3*b*). Based on our assumption that the maximum dispersal distance of animals scales with body mass, the ability to connect a landscape follows the same allometric scaling (figure 3*c*). Despite this dispersal advantage, intermediate-sized and large animal species (figure 3*a*, red to blue lines) lose biomass in landscapes in which they still have the potential to fully connect (almost) all habitat patches (figure 3*c*). The differences in plant species biomass densities cannot be attributed to body mass dependent species-specific dispersal distances as for plants maximum dispersal distances were randomly assigned, and thus, there is no connection between body mass and landscape connectance (ρ_i, figure 3*d*). Additional simulations, in which we assumed a constant maximum dispersal distance for all species of $\delta_i = \delta_{max} = 0.5$, support the negligibility of species-specific differences in dispersal ability for the emerging diversity patterns (see the electronic supplementary material, figure S3).

4. Discussion

Habitat fragmentation is a major driver of global biodiversity decline. To date, a comprehensive understanding of how the different aspects of habitat fragmentation, i.e. habitat loss [6], number of fragments and isolation, affect the diversity patterns of species embedded in complex ecological networks such as food webs is lacking (see e.g. meta-analysis by Martinson & Fagan [15], and references therein). Our simulation experiment allows us to independently explore the effects of number of fragments (i.e. number of habitat patches in the landscape), and of habitat isolation (i.e. distance between patches) on persistence and biomass densities of species in complex communities. We identified habitat isolation to be responsible for species diversity decline both at the local and regional scale.

The rate at which a species loses biomass density strongly depends on its trophic position. Large-bodied consumer species at the top of the food web are most sensitive to isolation although they are dispersing most effectively (i.e. for them, increasing distances between habitat patches do not necessarily result in the loss of dispersal pathways or a substantial increase of dispersal mortality). Surprisingly, we find top species to lose biomass density and sometimes even go extinct in landscapes they can still fully connect, whereas the biomass densities of small consumer species at lower trophic levels and plant species are only marginally affected by increasing habitat isolation. We attribute the accelerated loss of top species to the energy limitation propagated through the food web: with increasing habitat isolation an increasing fraction of the biomass production of the lower trophic levels is lost owing to mortality during dispersal and is thus no longer available to support the higher trophic levels. Additionally, the reduced top-down pressure on smaller consumers seems to compensate for their increased dispersal loss. Our model adds a complementary perspective to previous research pointing towards a trophic-dependent extinction risk owing to constraints in resource availability with increasing habitat fragmentation [9,38].

(a) Habitat isolation drives species loss

The increasing isolation of habitat fragments poses a severe threat to species persistence (but see [46,47]). We demonstrate in our simulation experiment that the generally observed pattern of species loss with increasing habitat isolation (e.g. [3]) also holds for species embedded in large food webs. The loss of species occurs both at the local ($\bar{\alpha}$-diversity) and regional (γ-diversity) scale. For the latter, however, an increase in β-diversity compensates the loss in local diversity ($\bar{\alpha}$) when landscapes become very isolated and γ-diversity increases again (see section below: Habitat isolation promotes β-diversity).

We modelled dispersal between habitat patches by assuming an energy loss for the dispersing organisms—a biologically realistic assumption as landscape degeneration, which often occurs concurrently with habitat fragmentation, increases the hostility of the habitat matrix [3]. Consequently, the dispersal mortality, and thus, biomass loss of populations to the habitat matrix increases substantially when dispersal distances between habitat patches expand. To account for the variation in dispersal ability among trophic groups, we incorporated species-specific maximum dispersal distances. For animal species, this maximum dispersal distance increases like a power law with body mass, therefore weakening the direct effect of habitat isolation the larger a species is. Despite this, top predators and other large consumer species respond strongly to isolation. These species exhibit a dramatic loss in biomass density or even go extinct in landscapes they still perceive as almost fully connected (landscape connectance, ρ_i, close to one), which indicates that their response to habitat isolation is mediated by indirect effects originating from the local food web dynamics.

(b) Local food web dynamics and energy limitation drive top predator loss

In local food webs, energy is transported rather inefficiently from the basal to the top species, with transfer efficiency in natural systems often only around 10% [48]. This energy limitation effectively controls the food chain length [26] and renders large species at high trophic levels vulnerable to extinction owing to resource shortage [49]. In our model, energy availability decreases if habitat isolation is high as this increases biomass loss during dispersal. This affects particularly small species at lower trophic levels because they generally have the highest metabolic costs per unit biomass and therefore the highest biomass losses per distance travelled [33,41]. The biomass loss during dispersal consequently reduces the net biomass production at the bottom of the food web and severely threatens species at higher trophic positions that already operate on a very limited resource supply.

Moreover, owing to the feedback mechanisms regulating the community dynamics within complex food webs, a loss of top consumer species can have severe consequences for the functioning and stability of the network [21,22]. A loss of top-down regulation can, for instance, lead to secondary extinctions resulting in simpler food webs [21,50]—an additional mechanism that can foster the loss of biodiversity as observed in our simulations. However, we also see a much more direct effect of the changing community composition: the biomass densities of small species that suffer most from increased dispersal mortality do not, as one might expect, decline much as isolation progresses. We attribute this to a release from top-down control as their consumers lose biomass or even go extinct, which counters the negative direct effect of habitat isolation. These arguments suggest that differential dispersal capabilities are less important than energetic limitations in explaining the strong negative response of large consumers to habitat isolation. This claim is supported

by the additional simulations where all species experienced the same level of dispersal mortality, which yielded similar results (see the electronic supplementary material, figure S3).

We did not find an effect of the number of patches on $\overline{\alpha}$-, β- and γ-diversity. As we model biomass densities on patches without defined area (see section below: Model specifications), fewer patches do not reflect habitat loss, but rather the loss of fragments, i.e. stepping stones in the dispersal network. Thus, the energy limitation in our simulated landscapes derives from direct dispersal loss and cascading effects of dispersal losses of resources. For plant and small animal species, this can be understood easily, as these species are less energy limited and thus are able to persist on a single habitat patch. For larger animal species the situation is more subtle: while they can integrate over multiple patches, feeding interactions still always occur on one patch at a time. If the biomass densities of their resources (and thus also the realized feeding rate) is too low on a particular patch to cover their metabolic requirements, they gain no advantage from the addition of more patches with equally low resource abundance.

(c) Habitat isolation promotes β-diversity

Contrary to the decline in $\overline{\alpha}$-diversity with increasing habitat isolation, we find an increase in β-diversity starting from around $\log_{10}$ mean patch distance $\overline{\tau} \approx -0.5$. We assumed identical abiotic conditions on all habitat patches, i.e. there are no differences in nutrient availability or background mortality rates. Therefore, any differences in conditions experienced by the species on different patches can only originate from the initial community composition and the structure of the dispersal network. One way for such different conditions to emerge is the disintegration of the dispersal network into several smaller clusters. Up to a $\log_{10}$ mean patch distance $\overline{\tau} \approx -0.5$, the species with the largest maximum dispersal distance (which could be both large animals that have not already gone extinct and plants with a randomly selected large dispersal distance) have a landscape connectance (ρ_i) of at least 0.5. This dispersal advantage easily allows them to connect all patches to a single network component, thereby providing homogenization for the meta-food-web. However, as the mean patch distance increases further, even these species cannot bridge all gaps in the habitat matrix any more and clusters of patches emerge that are for all species disconnected from the other patches. As these clusters vary in the number of patches and mean patch distance within the cluster, the level of dispersal mortality experienced by the species on the different clusters can also vary considerably. Any further increase in mean patch distance causes the landscape connectance to drop to nearly zero for all species and all patches within the landscape approach complete isolation. With no immigration into isolated patches, non-resident species cannot colonize them and initial community compositions drive dissimilarities among patches. However, the initial β-diversity is not sufficient in explaining the high β-diversity in strongly isolated landscapes (electronic supplementary material, figure S4). This suggests that different food web positions of initial species lead to different cascading effects in local food web dynamics with more or less secondary extinctions on isolated patches further increasing differences in local community compositions. The increase in β-diversity is even stronger than the loss of local diversity resulting in an increase in γ-diversity in highly isolated landscapes. However, species contributing to this high γ-diversity tend to occur on fewer patches and thus are more prone to go extinct in the whole landscape owing to stochastic extinction events.

(d) Model specifications

The framework we propose here for modelling meta-food-webs is very general and allows for a straightforward implementation of future empirical insight where we so far had to rely on plausible assumptions. The trophic network model for the local food webs is based on a tested and realistic allometric framework [41] with a fixed number of 40 species—a typical value in dynamic food web modelling (e.g. [51,52]). We based all model parameters on allometric principles [33,53] allowing for a simple adaptation of our modelling approach to other trophic networks such as empirically sampled food webs [54] or other food web models such as the niche model [55]. Moreover, empirical patch networks (e.g. the coordinates of meadows in a forest landscape) or other dispersal mechanisms [6,56] may be incorporated in the future. In our simulations, biomass loss during dispersal is predominantly responsible for the decline in species diversity. We linked the maximum dispersal distance of animals and thereby also their mortality during dispersal to body mass, which is plausible because larger animal species can move faster [34], and thus, have to spend less time in the hostile habitat matrix. Interestingly, however, we did not find any empirical study relating body mass directly to mortality or biomass loss during migration. If such information becomes available in the future, it can be easily incorporated into our modelling framework. Further, we deliberately assumed all habitat patches to share the same abiotic conditions [57] as we wanted to focus on the general effects of the interaction of complex food web and dispersal dynamics. Adding habitat heterogeneity among patches, e.g. by modifying nutrient availability or mean temperature, however, is straightforward and can be expected to yield additional insight into the mechanisms for the maintenance of species diversity in meta-food-webs. Finally, by using a dynamical model formulated in terms of biomass densities instead of absolute biomasses (or population sizes), we make the implicit assumption that patches do not have an absolute size. Thus, the number of patches in a landscape cannot be directly linked to the total amount of habitat but rather reflects the number of fragments, i.e. stepping stones in the dispersal network of a species. A decreasing number of patches thus does not necessarily imply habitat loss. In order to also address effects of habitat loss (in terms of area), the model could be adapted to include, for example, area-specific extinction thresholds and absolute biomasses in dispersal dynamics, but this was beyond the scope of this study.

(e) Synthesis and outlook

Our simulation experiment demonstrates that habitat isolation reduces species diversity in complex food webs in general, with differences in the effect across trophic levels. In increasingly isolated landscapes, energy becomes limited, which decreases the biomass density of large consumers or even drives them extinct. These primary extinctions may result in a cascade of secondary extinctions, given the importance of top predators for food web stability [24,58]. The increased risk of network downsizing, i.e. simple food webs with fewer and smaller species [14,59], stresses the importance to consider both direct and indirect trophic interactions as well as dispersal when assessing the extinction risk of species embedded in complex food webs and other ecological networks.

To date, most conservation research focuses on single species and does not consider the complex networks of interactions in natural communities [7,14]. However, the patterns we presented here clearly support previous studies highlighting the importance of trophic interactions (e.g. [9,37,38]). We show that the fragmentation-induced extinction risk of species strongly depends on their trophic position, with top species being particularly vulnerable. Given that top-down regulation can stabilize food webs [24,58], the loss of top predators might entail unpredictable consequences for adjacent trophic levels, destabilize food webs, reduce species diversity and trophic complexity and ultimately compromise ecosystem functioning [23,24]. In addition to the trophic position of a species, the trophic structure of the food web has also been shown to be an important aspect [11]. Our results suggest that bottom-up energy limitation caused by dispersal mortality owing to habitat isolation can be a critical factor driving species loss and the reduction of trophic complexity. The extent of this loss strongly depends on the spatial context (see also [6]). Thus, to maintain species-rich and trophic-complex natural communities under future environmental change, effective conservation planning must consider this interdependence of spatial and trophic dynamics. Notably, conservation planning should also consider habitat isolation and matrix hostility (and consequently dispersal mortality) to ensure sufficient biomass exchange between local populations, capable of inducing spatial rescue effects and to alleviate bottom-up energy limitation of large consumers. Energy limitations can also result from habitat loss (which we did not model here), decreasing energy availability at the bottom of the food web affecting local dynamics intrinsically independent of dispersal. Thus, avoiding habitat loss remains a crucial aspect [2,47]. We highlight the need to explore food webs and other complex ecological networks in a spatial context to achieve a more holistic understanding of biodiversity and ecosystem processes.

Data accessibility. We enable full reproducibility of our study by providing the original C- and R-code on the Dryad Digital Repository at: https://doi.org/10.5061/dryad.c624907 [60].

Authors' contributions. All authors conceived and designed the modelling framework; J.H. and R.R. ran the simulations on the high-performance-cluster; R.R. analysed the data with support from all other authors; all authors contributed to interpreting the results; J.H. wrote the first draft of the manuscript with support from R.R. and M.S.; and J.H. and R.R. led the editing. All authors contributed critically to the drafts and gave final approval for publication.

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2 | Research Chapter 2

A Bayesian network approach to trophic metacommunities shows habitat loss accelerates top species extinctions

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METHODS

A Bayesian network approach to trophic metacommunities shows that habitat loss accelerates top species extinctions

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Abstract

We develop a novel approach to analyse trophic metacommunities, which allows us to explore how progressive habitat loss affects food webs. Our method combines classic metapopulation models on fragmented landscapes with a Bayesian network representation of trophic interactions for calculating local extinction rates. This means that we can repurpose known results from classic metapopulation theory for trophic metacommunities, such as ranking the habitat patches of the landscape with respect to their importance to the persistence of the metacommunity as a whole. We use this to study the effects of habitat loss, both on model communities and the plant-mammal Serengeti food web dataset as a case study. Combining straightforward parameterisability with computational efficiency, our method permits the analysis of species-rich food webs over large landscapes, with hundreds or even thousands of species and habitat patches, while still retaining much of the flexibility of explicit dynamical models.

Keywords

Bayesian network, habitat loss, metacommunity, spatial food web.

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INTRODUCTION

Global biodiversity loss progresses at a rapid pace, with human-induced landscape changes such as habitat fragmentation and habitat loss being important drivers (Tylianakis *et al.*, 2008; Haddad *et al.*, 2015). To accurately forecast species extinction rates and develop efficient conservation strategies, ecologists must understand how species respond to these changes in habitat. Changes in the spatial configuration of a landscape drive species extinctions both directly but also through their effect on the interactions among species (Tylianakis *et al.*, 2008; Valiente-Banuet *et al.*, 2015). Their direction and extent is difficult to predict however, especially when considering complex ecological communities such as food webs.

Species in the same food web are inextricably linked, both directly and indirectly. Therefore, the extinction of one species can lead to a cascade of secondary extinctions which might affect the entire network (Ebenman and Jonsson, 2005; Dunne &Williams, 2009). This can have unpredictable consequences for the community as it might drastically change its structure and, at worst, lead to a highly impoverished community (Eklöf and Ebenman, 2006; Dunne and Williams, 2009).

Theoretical studies typically consider secondary extinctions in food webs without taking their spatial extent into account (Eklöf and Ebenman, 2006; Dunne and Williams, 2009; Staniczenko *et al.*, 2010; Binzer *et al.*, 2011; Curtsdotter *et al.*, 2011; Brose *et al.*, 2017). In non-spatial webs, the main approaches to model secondary extinctions are purely topological models, solely based on food web structure (Dunne and Williams, 2009), and dynamical models, which explicitly simulate population dynamics using a system of differential equations (Binzer *et al.*, 2011; Curtsdotter *et al.*, 2011). A middle-ground approach between them are Bayesian networks (Eklöf *et al.*, 2013; Box 1).

Predictions derived from non-spatial studies are crucial for understanding how species extinctions reverberate through food webs and how this affects their persistence and stability. Yet, by neglecting the spatial context, they also neglect the potentially strong impact spatial aspects can have on (local) communities (Gibert and Yeakel, 2019). Therefore, non-spatial food web models might miss important ecological patterns and processes that play out at the landscape level such as spatial rescue effects, the co-distribution of predators and their prey, species range limits and the restructuring of food webs considering different spatial scales (Guzman *et al.*, 2018). Using a spatially implicit model, Gravel *et al.* (2011a) for example showed that regional dynamics could promote the persistence of species in complex food webs that were locally prone to extinctions.

More recently, several advances in food web ecology address the effect of spatial change on food webs (Pillai *et al.*, 2011; Eklöf *et al.*, 2012), mostly however in small food webs and/or landscapes. For example, Liao *et al.* (2016, 2017a,2016) studied how the loss of habitat patches and landscape fragmentation affect food chains and simple food web motifs. An explicit population dynamical approach was taken by Ryser *et al.* (2019), who theoretically studied complex food webs in fragmented landscapes and found that habitat isolation drives top species extinctions due to bottom-up energy limitation. Using a system of differential equations, Ryser *et al.* (2019) explicitly simulate feeding and dispersal dynamics which allows for greater biological realism but also restricts the network sizes that are computationally feasible (Box 1).

Box 1. Secondary extinctions in non-spatial food web models

Topological models provide the simplest approach to understanding secondary extinctions in food webs: a species undergoes secondary extinction once all its resources go extinct, otherwise it is extant. This method only requires the network structure as input, so it can be used to model very large networks (Dunne and Williams, 2009). However, the assumption that species' extinction risks do not respond at all to either the identity or the number of resource species lost until the last of them is gone (at which point the extinction probability suddenly jumps to certainty) is rather crude.

Dynamical models are on the other end of the spectrum and offer a highly detailed description of trophic communities. They explicitly model population dynamics using a system of coupled ordinary differential equations (Berlow *et al.*, 2009; Binzer *et al.*, 2011; Curtsdotter *et al.*, 2011; Riede *et al.*, 2011). They depend on a large number of parameters and specific model assumptions, and are computationally expensive. Furthermore, while these models have the potential to be the most realistic of all, this potential is only realised if all model parameters are realistically represented. Although the rise in computational power promoted their use, the explicit modelling of population dynamics limits the food web size (and, in a spatial context, landscape size; Ryser *et al.*, 2019) that they can be applied to.

Bayesian network models (Eklöf *et al.*, 2013) provide a middle-ground between the two methods above. Bayesian networks permit extinction probabilities to increase gradually with resource loss, and allow them to be non-zero even when species have full access to their resources (quantifying the probability of species going extinct for causes other than those represented by the network). The numerical evaluation of Bayesian networks is highly efficient. This greatly reduces computation times and permits analysis of large food webs with hundreds or even thousands of species (and, in a spatial context, habitat patches).

In a Bayesian network, if a consumer species C has two prey items A and B whose extinction probabilities $P(\neg A)$ and $P(\neg B)$ are known, then one can obtain the marginal extinction probability $P(\neg C)$ of the consumer using the law of total probability:

$$\begin{aligned} P(\neg C) \quad &= P(\neg C|AB)P(A)P(B) + P(\neg C|\neg AB)P(\neg A)P(B) \\ &+ P(\neg C|A\neg B)P(A)P(\neg B) + P(\neg C|\neg A\neg B)P(\neg A)P(\neg B) \end{aligned} \tag{B1}$$

(this generalises straightforwardly to more than two prey items). Here $P(A) = 1 - P(\neg A)$ (and similarly for species B), and the conditional probabilities are determined from some set of model assumptions. One such assumption is that the probability $P(\neg C|f)$ of a species C going extinct is a function of just the fraction f, and not the identity, of its resources that are absent (see the Supporting Information, Section S7 for a generalisation, where each prey contributes a different amount to the consumer's diet):

$$P(\neg C|f) = \pi_C + (1 - \pi_C)w(f) \tag{B2}$$

where π_C is species C's baseline extinction probability (the likelihood of extinction despite all its resources being present), and the weighting function $w(f)$. is monotonically increasing in f. such that $w(0) = 0$ and $w(1) = 1$. For a basal species A, we assume its abiotic resources are always available ($f = 0$), so $P(\neg A) = \pi_A + (1 - \pi_A)w(0) = \pi_A$. For a non-basal species C, one obtains $P(\neg C)$ by using the already calculated extinction probabilities of its prey, and then applying eqn B1. Thus, determining the extinction probabilities of all species in a food web is a bottom-up calculation process: we start with basal species, then move on to species only consuming those basal species, and so on.

This also means that the Bayesian network approach has two important limitations. First, the food webs must be acyclic, otherwise this bottom-up approach would not work. Second, since predators are influenced by their prey but prey dynamics do not depend on the presence of their predators at all, the method cannot capture any top-down effects (a property shared with topological models).

To be able to explore much larger systems, here we develop a novel approach to study trophic metacommunities which is rooted in single-species metapopulation models on fragmented landscapes (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001; Hanski and Ovaskainen, 2003; Grilli *et al.*, 2015). The essence of our method is that species' extinction rates are calculated from a Bayesian network representation of the food web (Eklöf *et al.*, 2013), which allows us to model food webs with hundreds of species and patches. Our approach can also be used for obtaining analytical solutions for simple community modules (Supporting Information, Section S4). The method retains many known properties of metapopulation theory, such as being able to rank the habitat patches of the landscape with respect to their importance to the persistence of the metacommunity Ovaskainen and Hanski, 2001). We make use of this ranking to study how progressive habitat loss affects species extinctions, depending on whether one prioritises the removal of valuable vs. non-valuable patches.

The article is structured as follows. After briefly presenting our modelling framework and its parameterisation (Section 2), we use it to study the effect of habitat loss on community persistence —first on model food webs (Section 3), then in a case study on an empirical example (Section 4). We finish by reflecting on the advantages and limitations of our approach, and its place in the wider context of trophic metacommunity theory (Section 5).

METHODS

Model summary

Our starting point is a spatially explicit, Levins-type metapopulation model over a fragmented landscape consisting of N habitat patches connected by dispersal (Hanski and Ovaskainen, 2000, 2003; Ovaskainen and Hanski, 2001; Grilli *et al.*, 2015). Each of S species has a metapopulation over this landscape. Colonisation depends on species' current patch occupancies and dispersal abilities, and is unaffected by interspecific interactions. Extinctions, on the other hand, happen both due to local patch conditions and the fact that the species form a trophic network: extinction risk in a given patch increases when more prey items of a species are locally absent. We do not consider non-trophic interactions here.

More formally, we model the probability p_i^k that species i is found in patch k. (Here and elsewhere, subscripts refer to species and superscripts to patches.) Colonisation rates of patch k by species i, $C_i^k = \sum_{l=1}^{N} M_i^{kl} p_i^l$, are modelled using a species-dependent landscape matrix whose (k,l) th entry M_i^{kl} gives the dispersal rate of species i from patch l to k. In turn, extinction rates are obtained from the probability δ_i^k that species i disappears from patch k. As metapopulation models assume that migration operates on a slower time scale than local population dynamics (Hanski, 1994), we assume that within-patch extinction rates are not affected by the occupancy rates of other patches, so that within-patch extinction can be modelled as a Poisson process with rate E_i^k. So the probability of extinction occurring within one unit of time is $\delta_i^k = 1 - \exp\left(-E_i^k\right)$, from which $E_i^k = -\log\left(1-\delta_i^k\right)$. With these colonisation and extinction rates, the model reads (Supporting Information, Section S2):

$$\frac{dp_i^k}{dt} = \left(1-p_i^k\right)\sum_{l=1}^{N} M_i^{kl} p_i^l + p_i^k \log\left(1-\delta_i^k\right) \quad (i=1,\ldots,S;\ k=1,\ldots,N) \tag{1}$$

The central idea of our approach is to couple these independent metapopulation equations by making the extinction probabilities δ_i^k depend on the local persistence probabilities of species i's prey items via a Bayesian network representation of the food web (Eklöf *et al.*, 2013). When modelling species extinctions using Bayesian networks, each species i in patch k has a baseline probability of extinction π_i^k; the species goes extinct with this probability even if it has full access to its resources. Second, the conditional probability of a species to go extinct in a patch depends on the fraction f of its resources that are locally absent. This conditional probability increases monotonically with f, from the baseline probability π_i^k to certainty as f increases from 0 to 1. The marginal probability δ_i^k is then obtained by substituting all conditional probabilities into the law of total probability (Box 1; Supporting Information, Section S1).

The model retains many known results from the classic metapopulation theory on which it is based. We can determine the persistence of any species i by its metapopulation capacity λ_i: if this quantity exceeds 1 it means that the metapopulation persists at equilibrium, otherwise all p_i^k are zero. For eqn 1, λ_i is given by the leading eigenvalue of the matrix $A_i^{kl} = -M_i^{kl}/\log\left(1-\delta_i^k\right)$ (Supporting Information, Section S3). Also, the relative patch value $V_i^k = \left(\lambda_i - \lambda_i^{-k}\right)/\lambda_i$ (where λ_i^{-k} is species i's metapopulation capacity after patch k is removed) can be obtained as the normalised product of the dominant left and right eigenvectors of A_i^{kl} (Ovaskainen and Hanski, 2001). This quantity measures how important a patch is for the persistence of a species. We use it to rank the patches of a landscape with respect to their importance to the persistence of the metacommunity.

Model parameterisation

We first constructed four model food webs via the allometric method of Schneider *et al.* (2016) (Supporting Information, Section S5.1). Each web has 400 species, but with a varying fraction of consumer to basal species (200:200, 250:150, 300:100, and 350:50). To study how progressive habitat loss affects these webs, we generated five landscapes, each with 300 uniformly distributed patches in the unit square. The landscape matrices were constructed by making their entries decline exponentially with the distance d^{kl} between patches k and l: $M_i^{kl} = \exp\left(-d^{kl}/\xi_i\right)$, where ξ_i is the characteristic dispersal distance of species i.

We assume homogeneous landscapes where all patches have the same abiotic conditions and each patch can potentially harbour the full food web. This means that both the baseline extinction probabilities π_i and dispersal distances ξ_i are patch-independent. Their species-dependence may take one of two forms. First, they can be constant across all species, with $\pi_i = 0.2$ and $\xi_i = 0.055$. Second, they may be trophic level-based. We calculated the trophic level T_i of each species i as a prey-averaged trophic level (Williams and Martinez, 2004; Supporting Information, Section S5.2). Denoting their arithmetic average by $\bar{T}$, we set $\pi_i = 0.2T_i/\bar{T}$ and $\xi_i = 0.055T_i/\bar{T}$. The numerical factors adjust the arithmetic average $\bar{\pi}$ and $\bar{\xi}$ to be equal to 0.2 and 0.055 respectively, for a better comparison with the constant case. Additionally, to explore the role of habitat connectivity in general, we gradually increased ξ_i from 0.01 to 0.1 (keeping it equal across species), and let π_i be trophic level-based (Supporting Information, Section S6).

We also looked at how the functional form of a consumer's response to the loss of resources affects the response of a food web to habitat loss, by implementing four different forms of the response function. All are described by regularised beta functions of the fraction f of resource species lost, with different shape parameters α and β:

(1) $\alpha = \beta = 1$ (linear function; see inset in top right corner of Fig. 3a). Here a consumer's probability of extinction is simply proportional to the fraction of resources lost.
(2) $\alpha = 5$, $\beta = 1$ (Fig. 3b). This is a convex function, meaning that consumer extinction probabilities only start appreciably increasing after some fixed fraction of the resources have already been lost.
(3) $\alpha = 1$, $\beta = 5$ (Fig. 3c). A concave function: consumer extinction probabilities attain high values even after the removal of a small fraction of their prey.
(4) $\alpha = \beta = 5$ (Fig. 3d). A sigmoidal function, combining properties of the convex and concave cases.

Implementing habitat loss

First, we obtain the equilibrium patch occupancies for each food web on each landscape. We do so beginning with the basal species (for whom $\delta_i^k = \pi_i^k$), by solving for their equilibrium state in eqn 1 (Supporting Information, Section S3). We use these occupancy data and the Bayesian network representation of the food web (Box 1) to obtain their δ_i^k. With these parameters, we then solve eqn 1 for all those species consuming only basal ones. We then obtain their δ_i^k in turn, and go on to solve for the patch occupancies of species consuming only basal and primary consumer species—and so on, until top predators are reached (Supporting Information, Section S1–S2).

We start implementing habitat loss if at least one consumer species persists. We do this by gradually removing patches from each landscape, always 10 at a time. The order of removal differs between three habitat loss scenarios:

(1) Best-case scenario: patches are removed in increasing order of patch value (least valuable patches first). Since species at different trophic positions may differ in which patches are most valuable to them, we rank the patches based on the patch values of basal species.
(2) Worst-case scenario: as above, but removing patches in decreasing order of patch value (most valuable first).
(3) Random scenario: patches are removed at random.

The patch ranking formula only applies for small perturbations of the landscape. Therefore, after each patch loss step (simultaneous removal of 10 patches), we recalculate the patch values to re-rank the order in which we will remove patches next. We repeat this process until either all but basal species have gone extinct, or less than two patches remain in a landscape. Figure 1 illustrates the habitat loss scenarios by displaying the patch occupancies for a basal species and a top predator over a landscape.

For the linear functional form of predator response to prey loss ($\alpha = \beta = 1$), we additionally looked at removing patches based on the patch value rankings of top species, instead of basal ones (Supporting Information, Section S6.2). This means that patch removal was stopped whenever the top species have gone extinct.

Finally, we have also implemented a numerical experiment where we remove the links connecting the patches, instead of the patches themselves. This was also done in a random, best-case, and worst-case sequence (Supporting Information, Section S9). Link removal expresses the assumption that individuals have more difficulty travelling across patches due to the deterioration of the habitat matrix, even though the patches themselves are intact.

RESULTS

Our approach can be used to obtain analytical approximations for the metapopulation capacities in simple food web structures (Supporting Information, Section S4). One such structure is a linear food chain (species 1 is the basal species eaten by species 2, which is in turn eaten by species 3, and so on, until the top species) over a homogeneous landscape (baseline extinction probabilities are patch-independent, $\pi_i^k = \pi_i$). In this case the following recursion equation approximates the metapopulation capacities λ_i:

$$\lambda_{i+1} \approx \frac{\lambda_{M_{i+1}}}{\lambda_{M_i}/\lambda_i - \log[(1-\pi_{i+1})(1-1/\lambda_i)]} \quad (2)$$

for all $i>1$, and $\lambda_1 = -\lambda_{M_1}/\log(1-\pi_1)$ for the basal species. λ_{M_i} is the dominant eigenvalue of species i's landscape matrix M_i^{kl}, which we do not assume to be generated by any particular kernel form here. We can simplify this expression further by assuming $\pi_i = \pi$ and $\lambda_{M_i} = \lambda_M$ are constant across species:

$$\lambda_{i+1} \approx \frac{\lambda_M}{\lambda_M/\lambda_i - \log[(1-\pi)(1-1/\lambda_i)]} \quad (3)$$

One can show that eqn 3 implies strictly decreasing metapopulation capacities with increasing trophic level, eventually dropping them below 1 (Supporting Information, Section S4.2). This imposes a limit on the maximum length of the trophic chain, because species persistence requires $\lambda_i>1$. The following simple approximation can be derived for the maximum number of trophic levels T:

$$T = -\lambda_M \log(\pi) \quad (4)$$

Empirical estimates of λ_M from three different butterfly metapopulations (Hanski, 1994) gave 3.9, 0.97, and 0.74 (Supporting Information, Section S4.2). If these are indeed typical values, then eqn 4 reveals that trophic chain length is quite restricted unless π is quite low (Fig. 2). For instance, with $\lambda_M = 2$ and $\pi = 0.1$, the number of trophic levels is already limited to 5 at most. The upshot is that, quite apart from energetic or other constraints, the simple realities of metacommunity structure alone can restrict the maximum possible number of trophic levels to a handful—a conclusion consistent with an earlier study employing a slightly different modelling approach (Calcagno *et al.*, 2011).

Beyond such simple food web structures, one can rely on numerical solutions to eqn 1, which we have done to explore our four large model food webs. Since they produce similar trends, we present results for the one with 300 consumer and 100 basal species (Fig. 3; see Supporting Information, Section S6 for the others). The extent to which habitat loss threatens species persistence differs significantly between patch removal scenarios. In the best-case scenario, unless consumer response to prey absence is described by a strongly concave function (Fig. 3c), species have a high chance to persist even if a large fraction of habitat patches are lost. This applies to species at all trophic levels, though metapopulation capacities are generally higher at lower levels. By contrast, in the random and worst-case scenarios, species across all trophic levels have a much higher risk of extinction even after moderate levels of habitat removal. Interestingly, it makes almost no difference whether habitat loss starts with the most valuable patches or occurs randomly. This means that random patch removal is practically as harmful to a metacommunity as if one intentionally tried to cause the greatest damage. This pattern was observed for all food webs, landscapes, and parameterisations, and highlights the importance of planned landscape alterations whereby only patches of low value are removed. Note however that when removing links between patches instead of the patches themselves, random removal

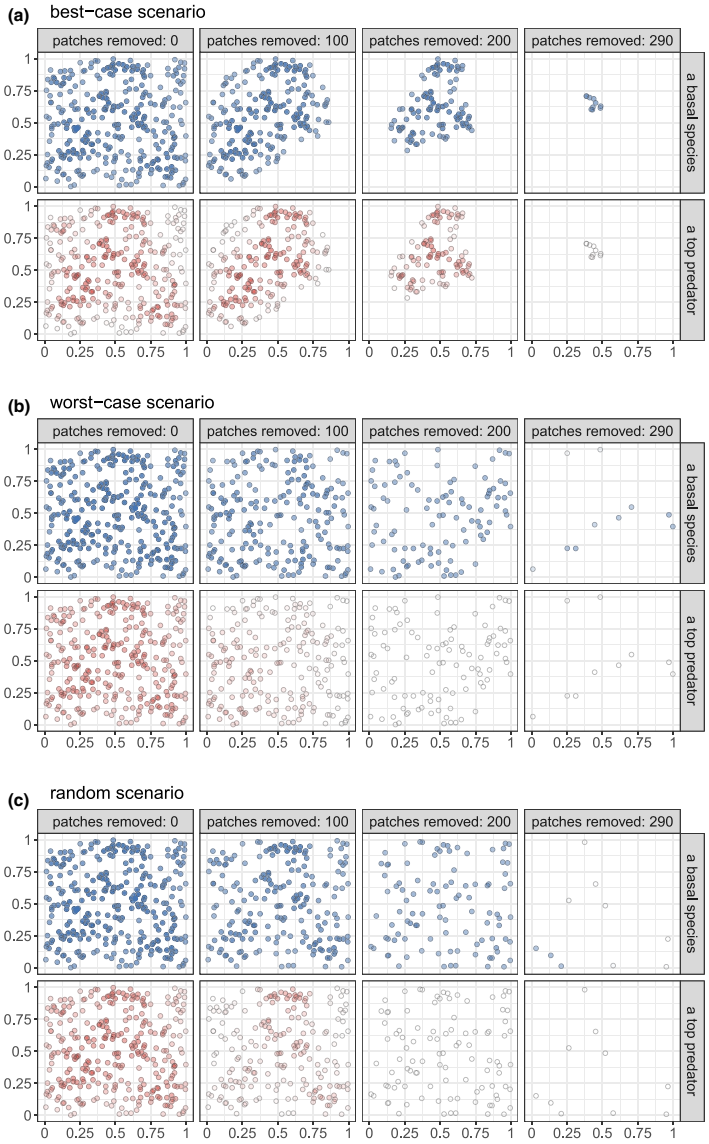

Figure 1 Patch occupancies along a habitat loss gradient, for a basal species (blue) and a top predator (red) in a model food web with 300 consumer and 100 basal species. Axes are coordinates of the landscape, circles are patches and their shading is proportional to local persistence probabilities (dark blue/red: 100% persistence; empty circle: 0%). In the best-case scenario (a), we first remove patches that contribute the least to the metapopulation capacity of the basal species; in the worst-case scenario (b), we start with patches that contribute the most; and in (c) we remove patches randomly. The dispersal distance ξ_i is 0.055 for all species, and baseline extinction probabilities π_i increase linearly with trophic level.

falls more in-between the best- and worst-case link removal scenarios, even though all other aspects of the results are qualitatively identical (Supporting Information, Section S9).

Both the baseline extinction probability π_i and dispersal distance ξ_i affect the described outcomes, but in most cases do not change the overall trends (Fig. 3). If π_i (but not ξ_i) increases with trophic level, differences in metapopulation capacity across trophic levels are elevated compared to the constant case, with higher values for lower trophic levels. When both π_i and ξ_i increase with trophic level (a likely scenario if trophic level and body mass are correlated, since larger-bodied organisms disperse faster and also tend to have

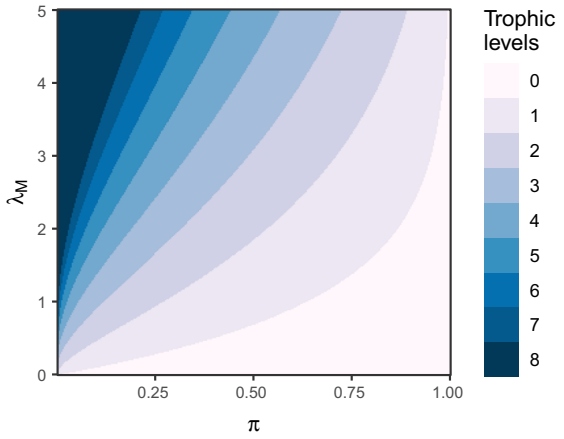

Figure 2 The maximum number of trophic levels in trophic chain metacommunities, as a function of a common baseline extinction probability π and the leading eigenvalue of a common landscape matrix λ_M. Unless π is low and λ_M simultaneously high, the metacommunity structure itself puts a cap on the number of possible trophic levels. This colour map was generated by iterating eqn 3 until metapopulation capacities dropped below the persistence threshold of 1. However, the same result is obtained by approximating the maximum number of trophic levels simply with $-\lambda_M \log(\pi)$ (eqn 4; see also Supporting Information, Fig. S3).

lower population sizes, increasing extinction risk), these differences are reduced, and metapopulation capacities start decreasing even after moderate habitat loss. Finally, when ξ_i but not π_i increases with trophic level, we find a reversed relationship between metapopulation capacity and trophic level for low to moderate habitat loss, with higher trophic levels now also having higher metapopulation capacities. In line with our Bayesian network approach which neglects top-down effects, species at the top of the food web generally have lower metapopulation capacities and are more likely to go extinct than species at lower levels. The reason we do not see this here is that the stronger landscape connectivity gained by faster dispersal at higher trophic levels offsets the increased risk of extinction due to local prey absence.

Note that, while we have assumed that dispersal ability is either constant or increases with trophic level, this need not be the case. In some systems, dispersal rates may actually decrease (Pedersen *et al*., 2016). Beisner *et al*. (2006) show evidence that zooplankton and fish (species at higher trophic levels) disperse more rarely than smaller organisms in lakes. Villarino *et al*. (2018) show the same phenomenon for plankton, based on body sizes. In such systems, one can implement dispersal rates that decrease with trophic level. All other things equal, this will further hinder the persistence of higher trophic levels.

Changing the functional form of a consumer's response to the loss of its resources alters the overall, absolute scaling of the metapopulation capacities, with little effect on their relative values (compare Fig. 3a–d). For functional forms leading to reduced metapopulation capacities, this means extinctions happen at lower numbers of removed patches. In the case of a concave response function for instance, we find that the highest trophic levels are often unable to persist even on a fully intact landscape. This is because their persistence probabilities are disproportionately reduced by the absence of even a few of their prey items.

Predictably, an overall increase in habitat connectivity, emulated by gradually increasing ξ_i from 0.01 to 0.1 (keeping it equal across species, and letting π_i be trophic level-based), acts as a general buffer against species extinctions up until habitat loss becomes too severe (Supporting Information, Section S6). Also, removing patches based on the patch value rankings of top species instead of basal ones does not alter the general patterns we observed, at least for the linear consumer response to prey loss we tested ($\alpha = \beta = 1$). The only difference is that, since patch removal is stopped whenever the top species go extinct, there is no information on metapopulation capacities beyond that point (Supporting Information, Section S6.2). Finally, we have also checked what happens over landscapes where patches are arranged in a more regular, grid-like manner than expected by chance (Supporting Information, Section S10). It turns out that more regular landscapes behave much like random ones; however, they lead to reduced metapopulation capacities overall, hindering metacommunity persistence.

A case study

We demonstrate that our framework can be readily applied to empirical systems using, as a case study, the plant-mammal Serengeti food web dataset (Baskerville *et al*., 2011). This is a species-rich web with the plant species mostly associated with particular habitats and mammals often tightly associated with well-defined plant groups (Baskerville *et al*., 2011). Although the Serengeti ecosystem is a protected area, there are nevertheless threats towards the habitat types within the system. First, the rapidly growing human population outside the park borders increase livestock grazing within the park, resulting in habitat degradation that is particularly severe near the borders (Veldhuis *et al*., 2019). Second, climate change has recently caused warmer and longer dry season as well as more powerful rains, resulting in soil erosion and washouts (Ritchie, 2008). As such, assessing the effects of habitat loss is relevant for the system. This, together with the data set's species richness and organisation into well-defined trophic levels, make it a good case study for demonstrating our method.

The Serengeti food web data set (Baskerville *et al*, 2011) contains a total of 161 species and 592 feeding links across three distinct trophic levels, with nine carnivore species feeding on 23 herbivore species feeding on 129 plant species. Apart from a single cannibalistic link (belonging to *Panthera leo*, the lion), the web is completely acyclic. Since the Bayesian network approach requires acyclic networks, we removed this self-link from the data.

In their work, Baskerville *et al*. (2011) used a modified version of the group model (Allesina and Pascual, 2009) and showed that the web contains functionally distinct groups of plants strongly associated with habitat types, connected to distinct groups of primary consumers that in turn are connected to distinct groups of secondary consumers. The nested

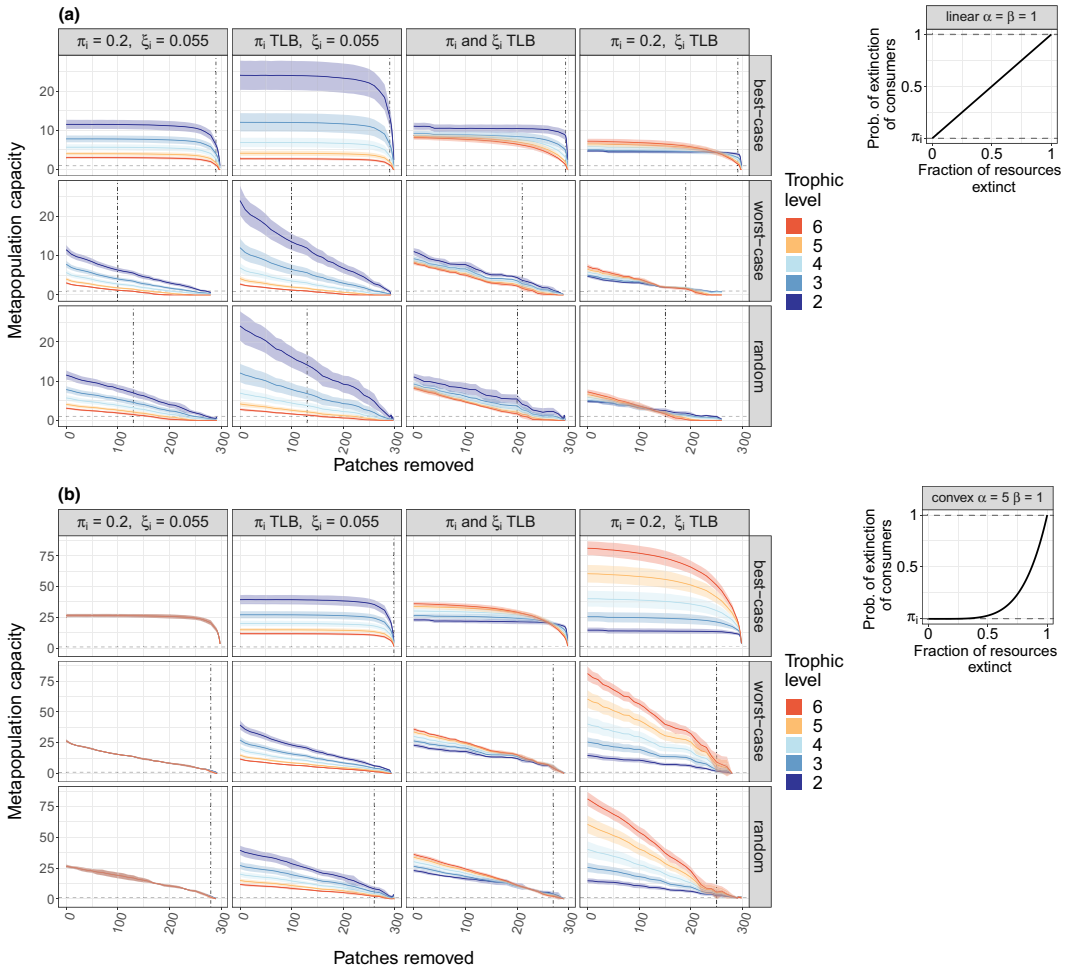

Figure 3 Effect of habitat loss on species persistence in a model food web with 300 consumer and 100 basal species. (a–d) are for different functional forms of a consumer's response to the loss of resources (top right insets). Species are grouped into trophic levels (colour legends); lines show the mean and the bands around them the one standard deviation range of the metapopulation capacities of species in the corresponding trophic level. Rows indicate patch removal scenario (best-case, worst-case and random); columns the parameterisation method: baseline extinction probabilities π_i and dispersal distances ξ_i can either take on one value across all species, or increase with trophic level (trophic level-based, TLB). Horizontal dashed lines highlight a metapopulation capacity of 1, the threshold for long-term species persistence. Vertical dashed lines show when the metapopulation capacity of the top species in the food web drops below this threshold.

network structure coupled to a spatial component, together with a high species richness, make the Serengeti food web a good case study to apply our method to. However, since there are only three distinct trophic levels in this system (with a strong bias towards basal species), we use the groups to parameterise our model in addition to the constant and trophic level-based parameterisations we relied on earlier (Supporting Information, Section S6). We follow the group labelling in Baskerville *et al.* (2011) and assign carnivores to groups 1-2, herbivores to groups 3-6, and basal species to groups 7-14. Since group labels decrease with trophic level but we would like both the baseline extinction probabilities π_i and dispersal distances ξ_i to increase with them, we define $\pi_i = 0.2(15 - G_i)/\bar{G}$ and $\xi_i = 0.055(15 - G_i)/\bar{G}$, where G_i is the group index and $\bar{G}$ their arithmetic average. While this particular parameterisation of groups within a trophic level does not have any specific ecological relevance, it demonstrates how parameter values can be assigned if, for example, ecological information on dispersal properties for certain groups of species is available.

The original dataset does not contain any explicit spatial arrangement of the food web in a landscape. Therefore we use

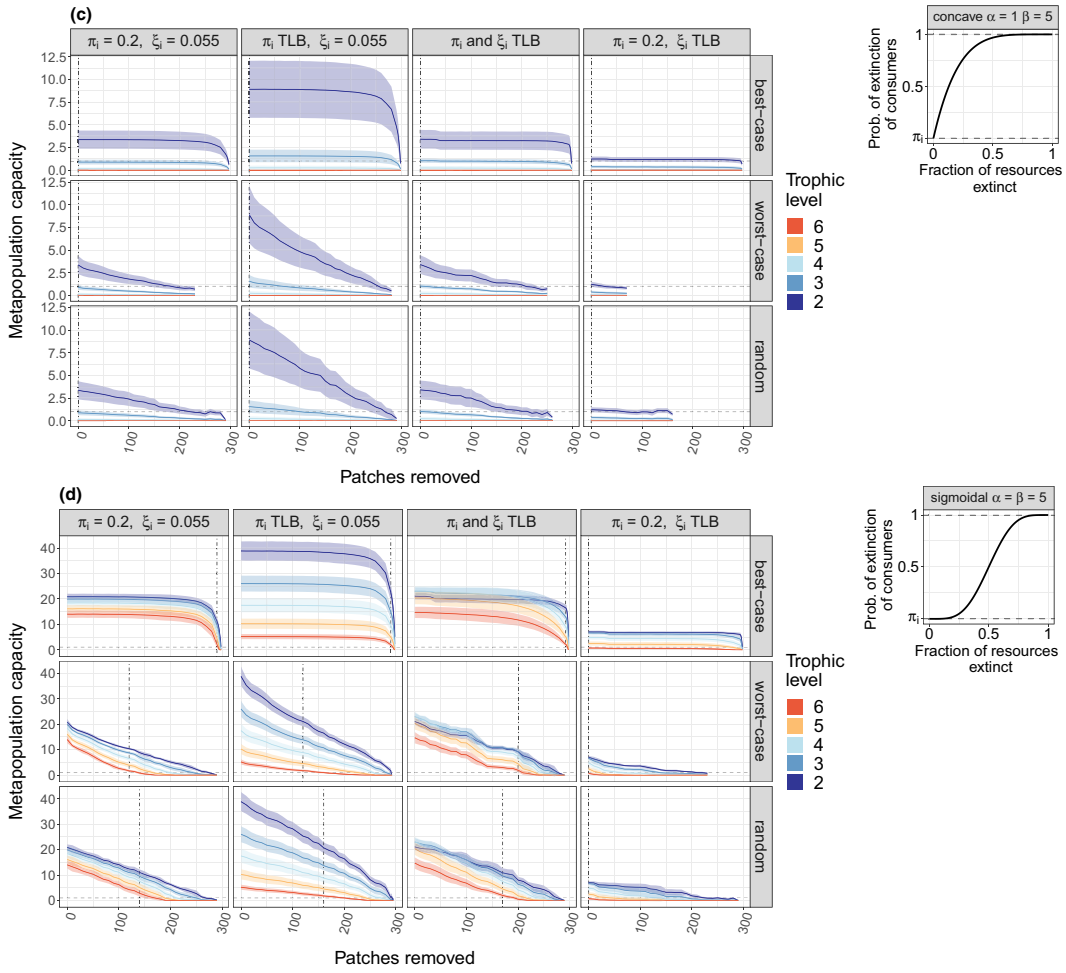

Figure 3 Continued.

the same approach here as for our model food webs and construct a landscape of 300 patches uniformly placed in the unit square. In the best- and worst-case habitat loss scenarios, we ranked patches for removal based on their contribution to the metapopulation capacity of a basal species. This species was chosen to be the Gum arabic tree (*Acacia senegal*), because it is a basal species that is also the sole member of spatial group 12.

The patterns we obtain for the Serengeti food web when π_i and ξ_i are constant or trophic level-based are consistent with the results found for the model food webs (Supporting Information, Section S6), with one exception. We find that the negative effect of a concave predator response on metacommunity persistence is strongly mitigated, with the metacommunity persisting even under severe habitat loss and a worst-case patch removal scenario. This is in contrast to the pattern seen in the model food webs, where the concave form immediately leads to the loss of the topmost trophic levels. However, this result is an artefact of the overabundance of basal species in the Serengeti dataset, and the low baseline extinction probability they all receive under a strictly trophic level-based parameterisation. When parameters are spatial group-based (Figure 4), the better resolution of the parameterisation leads to an outcome in line with those seen in the model food webs when both π_i and ξ_i are trophic level-based.

DISCUSSION

Understanding how habitat loss affects complex communities such as food webs remains a major challenge in ecology (Guzman *et al.*, 2018; Leibold and Chase, 2018). Due to indirect effects present in ecological networks, the extinction of one

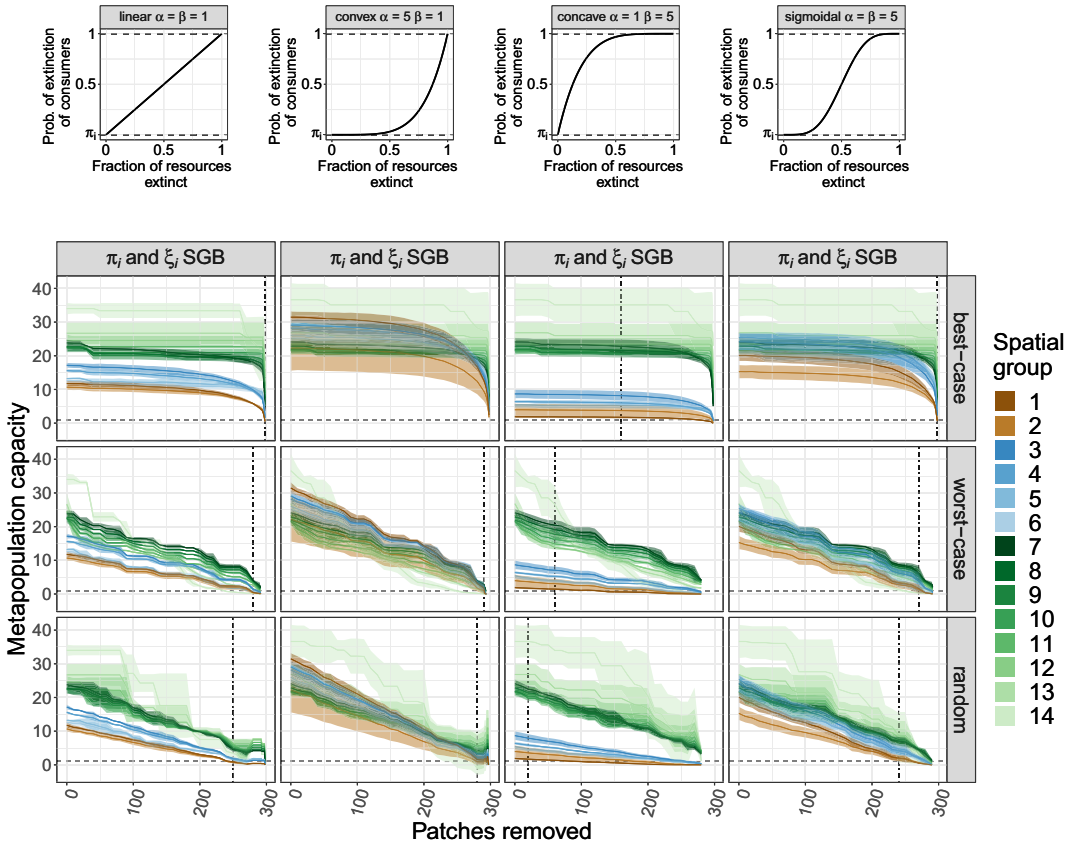

Figure 4 Effect of habitat loss on species persistence in the Serengeti food web. Layout as in Fig. 3, except colour legends show spatial group instead of trophic level, and columns show different functional forms of a consumer's response to the loss of resources (top insets). We show the results for the spatial group-based parameterisation (SGB), whereby both the baseline extinction probabilities π_i and dispersal distances ξ_i decrease with spatial group. In the colour scheme, green colours are groups whose species are primary producers, blue colours are groups with secondary consumers and brown colours are groups with top predators.

species can set in motion an entire cascade of secondary extinctions (Ebenman and Jonsson, 2005; Dunne and Williams, 2009). Here we have studied the effect of habitat loss on food webs by developing a novel approach to trophic metacommunities, combining the methods of classic metapopulation models on fragmented landscapes (Hanski and Ovaskainen, 2000, 2003; Ovaskainen and Hanski, 2001; Grilli *et al.*, 2015) with a Bayesian network representation of trophic interactions (Eklöf *et al.*, 2013) for calculating local extinction rates. The approach has much of the flexibility of explicit dynamical models (Ryser *et al.*, 2019), but is close in tractability and computational efficiency to simple topological methods (Dunne and Williams, 2009). This allows one to apply it to much larger food webs and landscapes than would be feasible with fully fledged dynamical models, while still retaining the ability to make predator extinction a smooth function of prey absence (as in Cazelles *et al.*, 2015). It thus provides an alternative, complementary way of analysing spatial food webs.

Thanks to its origin in well-studied metapopulation models, the method inherits many of their useful analytical properties, such as the ability to rank habitat patches with respect to their value to the community as a whole (Ovaskainen and Hanski, 2001). We demonstrated the importance of this ranking by simulating the patch removal process, taking away patches in sequence based on their value. This has revealed that trophic metacommunities can tolerate substantial habitat loss if the least valuable patches are removed first. However, starting with the most important ones greatly accelerates collapse. Surprisingly, random removal of patches is almost indistinguishable in its effects from the worst-case scenario of removing patches in decreasing order of importance, leading to similar landscapes in which habitat is scattered randomly (Fig. 1). In contrast to this, removing less valuable patches

first in the best-case scenario preserved habitat islands in which species were able to persist even under severe habitat loss. This highlights the need to estimate patch rankings in real-life conservation efforts, and to either prioritise conserving high-value patches, or else to improve the value of others —e.g. by increasing habitat connectivity. Land use strategies which take these considerations into account can then substantially promote food web persistence, and especially prevent top species extinctions.

Our metacommunity approach is similar to some trophic models of island biogeography (Holt, 2009; Gravel *et al.*, 2011a,b). In fact, our work can be seen as an extension and a change of focus from these works. It is an extension in two ways. First, our model is spatially explicit. Second, it replaces the strict dichotomy of a predator either being able to colonise a patch or not at all (depending on whether at least one of its prey items are locally present) with a more gradual approach using Bayesian networks, in which the presence of a predator is a smoothly increasing function of the likelihood of its prey items being present. It is a change of focus in that we have concentrated on the effects of habitat loss in closed metacommunities, instead of species-area relationships and the effect of network metrics on regional persistence in an island-mainland setting.

Our framework characterises each species by (1) their position in the food web; (2) their patch-specific baseline extinction probabilities π_i^k; and (3) their dispersal kernel (which, in our case, was always chosen to be exponential with a species-specific dispersal distance ξ_i). In the literature, an increased risk of extinction has been related to various indicators such as high trophic level, large body size, and low abundance (Gaston and Blackburn, 1995; Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Davidson *et al.*, 2009; Lee and Jetz, 2011). In agreement with several previous studies (Kondoh, 2003; van Nouhuys, 2005; Eklöf and Ebenman, 2006; Curtsdotter *et al.*, 2011; Liao *et al.*, 2017b; Ryser *et al.*, 2019), we found that species at higher trophic levels indeed tend to suffer elevated extinction risks. Differences in other indicators can be accounted for through their effects on the species-level parameters π_i^k and ξ_i. For instance, if a patch can only support a small number of individuals of a given species, it has a higher chance of disappearing due to demographic stochasticity even when all its resources are present. Such a situation can be represented by increasing the species' patch-specific baseline extinction probability. While this can and should be done whenever adequate data are available to characterise each patch on the landscape, here we deliberately assumed all habitat patches to share the same abiotic conditions (Leibold *et al.*, 2004) and thus baseline extinction probabilities to be independent of patch identity. This allowed us to focus on the general effects of habitat loss.

Similarly, dispersal ability is crucial for persistence in fragmented landscapes; all other things equal, species that are good disperses are at an advantage. In our model, we can integrate different assumptions for the dispersal abilities of species by assigning species-specific dispersal distances and dispersal kernel forms. We have looked at constant dispersal distances across species, and also ones that increase with trophic level (and, in case of the Serengeti food web, scale with the spatial guild of a species). Ideally, detailed information on species-specific dispersal would be used to construct realistic dispersal kernel functions in conjunction with realistic habitat structures, as the combination have profound consequences for species persistence (Årevall *et al.*, 2018). This may include possibilities such as multiplying the dispersal kernel of each species by an overall size-dependent scaling factor. While data are scarce, it is conceivable that this factor is in fact inversely related to size, due to smaller organisms having more offspring that disperse, as well as having faster population dynamics. The interplay of such a scaling relationship with the direct size dependence of dispersal distances may alter the interpretation of Fig. 3.

However, regardless of such details, it follows from the structure of our model that habitat destruction likely affects species at the highest trophic levels the most, since apart from having fewer available patches for colonisation in the landscape, they must also cope with the problem of reduced prey availability. In line with this expectation, we found that habitat isolation deconstructed food webs from top to bottom, with species at higher trophic levels going extinct first (Ryser *et al.*, 2019; McWilliams *et al.*, 2019). Dispersal ability can also be seen as a measure of habitat connectivity, i.e. how well species can access habitat patches in general. This is particularly important as human land use practices causing habitat loss often also decrease the quality of the habitat matrix in which the patches are embedded (Bonte *et al.*, 2012). A decrease in matrix quality manifests itself in overall reduced dispersal likelihoods, whereby the kernel yields a lower dispersal rate for all distances, reducing the chance of successful colonisation between habitats (Eklöf *et al.*, 2012).

Despite its tractability, computational efficiency, and straightforward parameterisability, our metacommunity approach also has idiosyncrasies and important limitations. First, it should be noted that only extinction rates depend on species interactions, not colonisation rates. This may look strange, implying that a predator i may establish in a patch k that is devoid of any prey. That, however, turns out to be irrelevant, because the extinction probability δ_i^k of the predator in such a patch is equal to one. Thus, the extinction rate $E_i^k = -\log\left(1-\delta_i^k\right)$ is infinitely large, immediately negating the effect of the colonisation process (eqn 1). While incorporating interaction-dependent colonisation in the model is definitely a promising avenue for future development, the lack of this dependence does not undermine the model's results or applicability.

Second, throughout this work, we have made conditional predator extinction probabilities either a function of the fraction, or weighted fraction (Supporting Information, Section S7), of prey species lost. There may be cases when it is better to make them some absolute function of the available prey in a given location—such as for opportunistic feeders which consume anything within a certain size range. Fortunately, our model is extensible to deal with such scenarios (Supporting Information, Section S1), though at the cost of replacing eqn B2 with something more complicated.

Third, the calculation of extinction rates depends heavily on the assumption of the separation of time scales between extinction and colonisation: the Bayesian network method of calculating extinction probabilities assumes that there is no

chance of an extinction cascade within a patch being stopped by a colonist of a prey species arriving midway through. This essentially means that mass effects are assumed not to influence extinction dynamics. It also explicitly assumes that everything is in (quasi-)equilibrium when calculating local extinction rates, so our method might not be suited for calculating extinction debts or patch occupancy dynamics far from equilibrium.

Fourth, the food web structure must be acyclic (no "A eats B eats C eats A" scenarios), because the Bayesian network formalism can only be used for such webs. Fortunately, while real food webs are not perfectly acyclic, they are generally close, and there are ways of removing cyclic links from food webs in a robust way that has minimal effect on the rest of the web (Allesina *et al*., 2009; Eklöf *et al*., 2013).

Finally, an important limitation is that species' dynamics depend only on the persistence probabilities of their prey, not their predators. In real food webs, secondary extinctions can emerge bottom-up (if consumers lose their resources), and top-down, by resources responding to the loss of their consumers. Species may, for example, be locally predated to extinction (Huffaker, 1958; Schoener *et al*., 2001), and the loss of a predator can release a prey species which then grows to the point of eliminating other species in the web (Paine, 1966, 1974; Lafferty and Suchanek, 2016). However, since Bayesian networks operate on a strict bottom-up principle whereby prey influence their predators but not vice versa (from the perspective of prey, their predators might as well not even be present), extinctions resulting from top-down effects are not implemented in our framework. This is a severe limitation; moreover, there is no immediate, straightforward remedy that would unambiguously extend the model to take top-down effects into account. This has to be considered when interpreting its results and applying the method to empirical systems: if, in a given system, top-down effects are deemed important, other methods should be used instead.

The current consensus within community ecology is that new ways of thinking about trophic metacommunities are needed to move the field forward (Leibold and Chase, 2018; Guzman *et al*., 2018; Hirt *et al*., 2018). Here we offered one possible approach to this problem, rooted in classic metapopulation theory and the method of Bayesian networks. Due to its flexibility and ability to handle large systems, we see our approach as a stepping-stone along the way to a fuller understanding. Our numerical experiments demonstrate that preserving high-value patches increases the likelihood of community persistence, even under severe habitat loss. Increasingly isolated landscapes, on the other hand, accelerate species extinctions and particularly drive top species towards extinction, reducing trophic complexity. Using a different methodology, similar trends have been observed by Ryser *et al*. (2019); in fact, our model qualitatively reproduces their results (Supporting Information, Section S8). Our findings reinforce that trophic interactions, dispersal ability and the spatial configuration of patches are crucial when assessing the extinction risk of species in fragmented landscapes. We hope that our method will be of use to ecologists interested in metacommunity processes and to provide useful insights for real-life conservation efforts to preserve complex trophic communities.

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AUTHORSHIP

JH and GB contributed equally to the project and are joint first authors. JH, GB and AE conceived of the study; JH and GB developed the modelling framework; JH and GB wrote the manuscript and performed numerical studies; GB wrote the supplement and derived analytical results. All authors contributed to the final form of the manuscript.

PEER REVIEW

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DATA ACCESSIBILITY STATEMENT

Data and code to reproduce our results can be found at: https://doi.org/10.5281/zenodo.4028326

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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3 | Research Chapter 3

Invasive spread in meta-food-webs depends on landscape structure, fertilization and species traits

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Invasive spread in meta-food-webs depends on landscape structure, fertilization and species traits

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Abstract

Land use change and biological invasions collectively threaten biodiversity. Yet, few studies have addressed how altering the landscape structure and nutrient supply might promote biological invasions and particularly invasive spread (the spread of an invader from the place of introduction), or asked whether these factors interact with biotic interactions and invader properties. We here provide a holistic network-based approach (built on an explicit population dynamic meta-food-web model) that allows us to jointly consider relevant factors at the local and the landscape scale. We ask what landscape properties underlying food webs might facilitate invasions and in particular invasive spread, and how the emerging patterns are influenced by invader traits. We numerically simulated 6300 single-species invasions by plant and animal species in landscapes with random or clustered distribution of habitat patches and different levels of nutrient supply. In total, our simulation experiment yielded 69% successful invasions—71% in clustered landscapes and 66% in random landscapes, with the proportion of successful invasions increasing with nutrient supply. Clustered landscapes can facilitate invasive spread within a habitat cluster, but can also prevent invasive spread between clusters; whereas in landscapes in which habitat is randomly positioned invasive spread is generally stronger. Also, oligotrophic landscapes generally prevent invasive species establishment and further spread, in particular of species at higher trophic positions due to energy limitation. Successful invaders, however, might have more severe impacts in oligotrophic landscapes as they make up a larger fraction of biomass density and species than in eutrophic landscapes. In our simulations, good dispersal abilities drive the broad-scale spread of invasive species in fragmented landscapes. Our approach makes an important contribution towards a better understanding of what combination of landscape and invader properties may facilitate or prevent invasive spread in natural ecosystems. This might allow ecologists to more effectively predict and manage biological invasions.

1 Introduction

Globally, the number of invasive species increases without any sign of saturation (Seebens et al. 2017), raising concern for biodiversity loss and biotic homogenization (Ricciardi et al. 2017, Courchamp et al. 2017). Invasive species can have profound consequences, both positive and negative, on the ecosystems they invade (David et al. 2017 and references therein). Understanding which combinations of species, habitats and landscape structures most effectively facilitate or prevent biological invasions is thus hugely important (Frost et al. 2019), yet poorly understood. Biological invasions are complex processes that consist of several stages (introduction, establishment, dispersal to new sites, and subsequent spread (Sakai et al. 2001, With 2002, Pantel et al. 2017)). Thus, when and where alien species will successfully invade a new environment involves a complex combination of interacting factors. Firstly, it depends on

the 'invasiveness' of the alien species. Certain species characteristics like good dispersal ability, high reproduction rate and generalism are often associated with high invasiveness (see, for example, Sakai et al. 2001, Kolar and Lodge 2001, Van Kleunen et al. 2010 and references therein) Additionally, also the trophic position and other species-level network properties of the potential invader can play a key role (Frost et al. 2019 and references therein). Romanuk et al. (2009), for example, found that generalist species, that are either herbivorous or feed on species at different trophic levels, and have few predators are generally most successful in invading complex food webs. These findings are further supported by Baiser et al. (2010), showing that invasion success of a potential invader also depends on the state of the native community, in their study the connectance of model food webs. In other words, a 'recipient' community might either be able to resist invasion or facilitate it. This depends, for example, on its diversity (Shea and Chesson 2002, Fridley et al. 2007) but also on its competitive strength (Hart and Gardner 1997), and network properties such as its robustness, connectance, link density, modularity, and nestedness (Romanuk et al. 2009, Baiser et al. 2010, Frost et al. 2019). This 'invasibility' of a native community may also differ between alien species trying to invade it. For example, if there is a lack of unexploited niche space in the native community, the chance of alien species to become successful invaders is rather low (Shea and Chesson 2002, Pantel et al. 2017, Frost et al. 2019). In contrast, if an invader has few or no predators in the invaded community (enemy-release hypothesis), invasion success should be rather high, provided that there is sufficient resource availability. This points to an interaction between traits of invasive species and characteristics of the invaded communities that drive the invasiveness.

Invasion success, however, does not only depend on invader properties and species interactions but also on the abiotic environment and biogeographical landscape properties, such as the spatial configuration of habitat (With 2002, Pantel et al. 2017 and references therein). This landscape configuration can strongly affect species persistence and species diversity (Gilarranz and Bascompte 2012, Pantel et al. 2017) and as such the 'invasibility' of the native community (diversity-invasibility hypothesis) (Frost et al. 2019 and references therein). Furthermore, given that any of the different stages included in the invasion process (introduction, establishment, dispersal, spread) may be sensitive to landscape properties, the spatial configuration of habitat can strongly influence the performance of the invader (With 2002, Pantel et al. 2017 and references therein). For example, the potential for introduction and successful establishment of alien species can depend on the degree of spatial connectivity between the native and introduced habitat, the spatial distribution of resources, of other species, and of habitat availability and quality (see Pantel et al. 2017 and references therein). The further spread of an invasive species across

a novel landscape depends among other factors on habitat availability together with the connectivity of habitat patches for the invader, which in turn depends on its dispersal ability (With 2002, Hastings et al. 2005). In addition to these spatial properties, invasive spread also depends on the state of the native community (see, for example, Clergeau and Mandon-Dalger 2001).

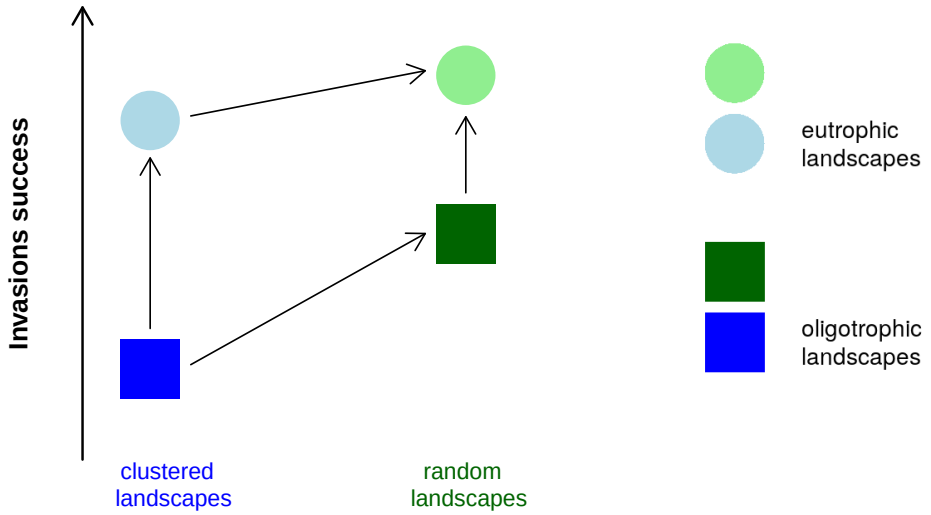
In addition to the spatial configuration of habitat, its quality in terms of nutrient availability can be another important determinant for invasion success. High nutrient availability generally causes higher population densities that are likely to facilitate establishment of invasive populations and thus their further spread through higher emigration rates. Also, nutrient availability has been shown to influence the number of trophic levels a landscape can generally support (Post 2002, Takimoto and Post 2013), and thus, a low nutrient availability may prevent the establishment of invaders at higher trophic positions. For example, oligotrophic landscapes with isolated habitat patches might favor invaders that can disperse over long distances and simultaneously can persist under such resource limited conditions. This means from a network perspective that whether an alien species becomes a successful invader depends on the number of links it can establish within the native community and the energy availability in the system to maintain a positive growth rate (Pantel et al. 2017). In general, link density and dispersal ability both depend on species traits such as body mass and movement mode (Jacob et al. 2011, Hirt et al. 2017a, 2018, Brose et al. 2019), opening up possibilities for trait-based generalizations of model approaches across species, communities and ecosystems.

However, so far, most of our knowledge of biological invasions comes from species-centered and/or trait-based approaches, trying to identify traits common to invasive species (see e.g., Cassey et al. 2004, Blackburn et al. 2009, Van Kleunen et al. 2010, David et al. 2017 and references therein). One frequent assumption is that traits associated with 'weedy' species such as a short generation time, high offspring production, potential long-distance dispersal and habitat and resource generalism facilitate invasion success (Kolar and Lodge 2001, Sakai et al. 2001, Cassey et al. 2004, Marvier and others. 2004). Although such approaches often consider abiotic drivers, focusing on particular traits and species, they lack ecological complexity in terms of species interactions and tend to ignore different causes of invasion (David et al. 2017). Similarly, most studies using spatial models to determine the spread of invasive species across a landscape (see the reviews by With 2002 and Hastings et al. 2005) and practices to slow their spread (Coutts et al. 2011) do not consider the plethora of (direct and indirect) species interactions. As a rare example, however, French and Travis (2001) could show that the presence of a competitor can reduce the rate of spread of invasion in a host-parasitoid system.

Both biotic interactions and abiotic conditions are important determinants for invasion success, and thus, categorizing successful invasive species by any unique set of traits has been proven difficult. This shows that accurately predicting biological invasions requires a holistic network-based approach, considering both biotic and abiotic drivers. While recent approaches more often make use of network theory to understand and predict biological invasions and incorporate the multiple directly and indirectly interacting species at different trophic levels (see, for example, David et al. 2017, Frost et al. 2019 and references therein), they often lack a spatial context (see, e.g., Romanuk et al. 2009, Baiser et al. 2010). To fill this gap, we here combine ecological and spatial networks to study what landscape properties render complex food webs more or less susceptible to invasion, and whether these properties interact with certain traits of alien species, such as their dispersal ability or trophic position (among others). To do this, we use a bioenergetic meta-food-web model adapted from Ryser et al. (2019). Following allometric scaling laws, the model combines feeding and dispersal dynamics of complex food webs in spatially-explicit patchy landscapes. This means body masses determine feeding links (who eats whom), their interaction strengths, the metabolic demands of species as well as the dispersal ranges for animal species (active dispersers), but not for plant species (passive dispersers). In other words, large animals are good dispersers and feed on plants and/or other animals that are smaller than themselves and can disperse over shorter distances. Hence, this framework allows us to explore the invasion success and invasive spread of alien species that vary in their dispersal ability and trophic position in landscapes differing in their landscape structure (random or clustered distribution of habitats) at different levels of nutrient supply (Figure 1).

Similar to food webs, in which nodes represent species and edges represent feeding links, fragmented landscapes can be described as networks, with nodes representing habitat location and edges distance or connectivity (Dale and Fortin 2010; Figure 1b). In such landscapes, species persistence depends to a large extent on a species' ability to connect the habitat patches of a landscape. This connectivity depends on the one hand on the spatial configuration of a landscape, i.e., how habitat is distributed in a landscape (here clustered or random), but also on the dispersal ability of a species (which here scales with body mass for animal species), determining its realized, species-specific spatial network (Hirt et al. 2018; Figure 1b, gray dashed lines). As long distances in clustered landscapes may prevent the spread of invasive species between clusters (Figure 1b), we expect higher spread of invasive species in random landscapes (Figure 1a, 1b). An increase in nutrient supply might not only facilitate establishment of invasive populations by higher resource availability but also increase the further spread through higher population densities that also yield higher emigration rates (Figure 1b). This might especially promote

(a)



(b)

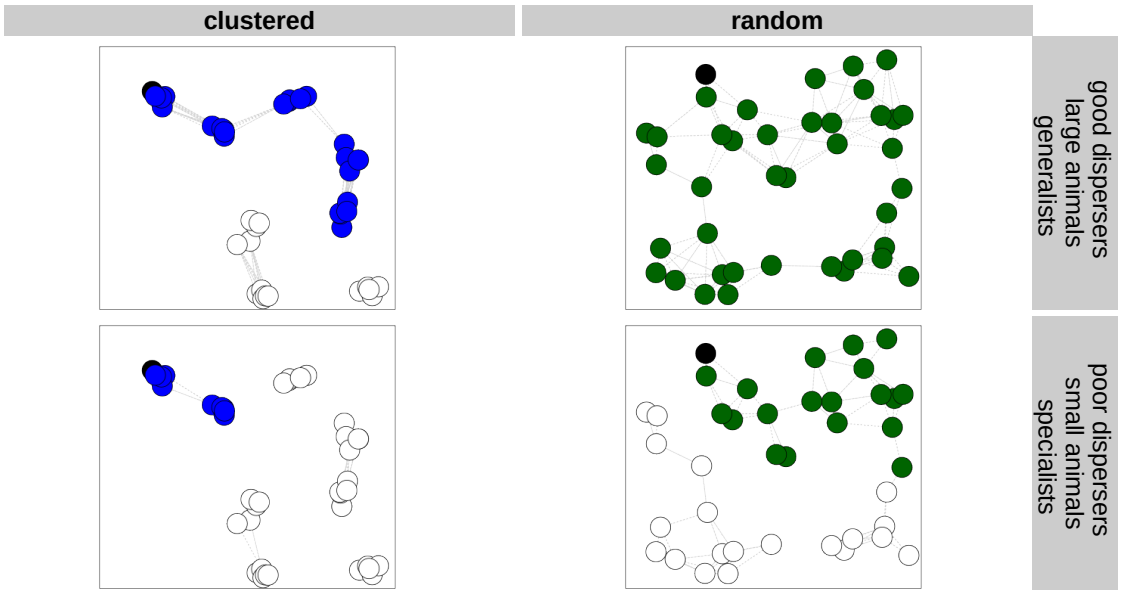


Figure 1: (a) Hypothesized effects of landscape properties on invasion success, here the fraction of invaded patches in a landscape (y-axis). Arrows indicate an increase in invasion success from clustered (blue) to random landscapes (green) and from oligotrophic (dark-colored squares) to eutrophic landscapes (light-colored circles). (b) Certain traits of invasive species might interact with landscape structure and nutrient availability in their effect on invasion success. Species with large dispersal ranges ('good dispersers', e.g., large animals, top row, for example, can better connect a landscape (gray dashed lines) and thus presumably spread further from the path of introduction (illustrated in black) than 'poor dispersers' (e.g., small animals, bottom row). Similarly, we expect generalist species that feed on various resources (top row) to have higher invasion success and spread rates than specialists feeding on few resources (bottom row).

the spread of invasive species at high trophic positions in clustered landscapes as they are presumably good dispersers but also depend on a sufficient nutrient supply in the landscape (Post 2002, Takimoto and Post 2013, Ryser et al. 2019). High dispersal ability of invaders is generally associated with high invasion success (Coutts et al. 2011), promoting their spread from the patch of introduction (Figure 1b, black patch) across the landscape (Figure 1b, blue and green patches, respectively). Invasive species with low dispersal ability on the other hand may be limited in the number of patches they can invade, especially so in clustered landscapes due to long distances between clusters. Additionally, species-level network properties such as the number of predators (vulnerability) and/or prey (generality) of an invasive species can impact their establishment and further spread across the landscape (Figure 1b). By combining food webs and networks of habitat patches our approach can improve the understanding of what determines invasion success and invasive spread in realistic ecosystems.

2 Methods

Model summary

We consider a multitrophic metacommunity consisting of 20 native plant and animal species and one invasive species (which can be a plant or an animal) on 40 homogeneous habitat patches, using a population dynamical approach based on the bioenergetic meta-food-web model by Ryser et al. (2019). The model combines an allometric trophic network model (Schneider et al. 2016) for the body-mass dependence of metabolism, growth and feeding with an allometric spatial network model (Hirt et al. 2018) describing the effect of the allometric scaling of dispersal distance on the realized connections between habitat patches. This means each species is fully characterized by its average adult body mass which determines its metabolic demands, its feeding links, the interaction strengths of these links, and its maximum dispersal distance (the latter only applies for animals). Habitat patches all share the same abiotic conditions and each patch can potentially harbor the full food web including the invader.

Local population dynamics We distinguish between animal species (trophic levels > 1) and plant species (trophic level 1) (see the SI, Figure S1a). For animal species, the rate of change in biomass densities on a patch are determined by biomass gains due to the consumption of animal and/or plant species, biomass losses due to being preyed upon by animals and metabolic demands (Table 1, Eq. T1.1). The rate of change in plant biomass densities on a given patch depends on growth due to the uptake of the two nutrients, mortality through grazing and metabolic losses (Table 1, Eq. T1.6). The energy supply for

the food web stems from an underlying nutrient model with two nutrients of different importance that drive the nutrient uptake and therefore the growth rate of the plant populations (Brose 2008, Schneider et al. 2016). The nutrient model consists of two nutrients of different importance, a nutrient turnover rate of 0.25 and a nutrient supply concentration (Table 1, Eq. T1.8). Applying different nutrient supply scenarios, we varied the nutrient supply concentration to obtain oligotrophic, mesotrophic and eutrophic landscapes (see *Generating landscapes*). See Table 1 for the corresponding equations and model parameters.

Dispersal dynamics Dispersal between habitat patches is integrated as a dynamic and species-specific process of emigration, traversing through the habitat matrix, and immigration. This means biomass flows dynamically between local populations based on the assumption that local population dynamics and dispersal occur at the same timescale (Amarasekare 2008), directly influencing each other (Fronhofer et al. 2018). To this end, we model emigration rate as a function of the local net growth rate, thereby summarizing resource availability, competition and predator pressure arising from local population dynamics (Table 2, Eq. T2.1). Immigration rates in turn, depend on the distance an organism has to travel to reach the next habitat patch, its species-specific dispersal range and on the quality of the matrix the habitat patches are embedded in (the habitat matrix) (Table 2, Table 2, Eq. T2.4). In line with previous theoretical frameworks and empirical observations (e.g., Holt 2002, Jetz et al. 2004, Holt and Hoopes 2005, Jenkins et al. 2007, Hirt et al. 2017a), we assume animals to be active dispersers and dispersal ranges to follow allometric scaling laws. Assuming that larger animals at high trophic positions are more mobile and have higher travel speeds, they can disperse further through the habitat matrix before they need to rest and feed in a habitat patch than smaller animals at lower trophic levels. To this end, we let maximum dispersal distances of animals scale with their body mass m_i (Table 2, Eq. T2.3). We use scaling parameters, so that the largest possible animal species with a body mass of $m_i = 10^{12}$ has a maximum dispersal range of $\delta_i = 0.5$ (half of the edge length of the landscape), whereas an animal species with the smallest possible body mass of $m_i = 10^2$ has a maximum dispersal range of $\delta_i = 0.158$ (see the SI, Figure S2). In contrast to animals, plant species are assumed to be passive dispersers (e.g., propagated by wind) (Jenkins et al. 2007), and thus, we sampled the maximum dispersal range of each plant species from a uniform probability density within the interval $(0, 0.5)$. This means the best plant disperser can potentially have the same maximum dispersal range as the largest possible animal species. By assigning species-specific maximum dispersal ranges, each species forms its own species-specific spatial network of habitat patches and thus perceives the same landscape differently (see the SI, Figure S3). Further, we

assume a hostile habitat matrix that does not permit feeding interactions during dispersal. Thus biomass is lost to the matrix during dispersal, scaling linearly with the distances traveled. Here this loss term depends on distance, however, it could also represent any other sort of dispersal loss. For numerical reasons, we did not allow dispersal flows below 10^{-17}. See Table 2 for the corresponding equations and model parameters.

Generating invasion webs

We generated five native food webs, each with 20 species, by randomly sampling the $\log_{10}$ body mass m_i of each species from a uniform probability density from the inclusive interval $(2, 12)$ for animal species, and from the inclusive interval $(0, 6)$ for plant species. For plant species (passive dispersers), we additionally sampled their maximum dispersal distances δ_i from a uniform probability density within the interval $(0, 0.5)$, whereas δ_i for animal species (active dispersers) scales with body mass. In this manner, we also determine the unique body mass and dispersal range of the invasive species k using the specified intervals for plants and animals respectively. Drawing species' body masses and the dispersal ranges of plant species at random makes the model inherently stochastic, but from thereon, all other steps are completely deterministic. For each food web, we simulate 21 single-species invasions of which five assume plant invaders and 16 animal invaders that differ in their body mass, trophic position and dispersal range.

Generating landscapes

To test the effect of the spatial habitat configuration (landscape structure) on invasion success, we generated a total of 20 landscapes with an edge length of 1, each comprising 40 habitat patches. In half of them, we distributed patches randomly in the landscape by sampling their x- and y-coordinates from a uniform distribution within the limits (0, 1) (random landscapes). In the other half, we randomly distributed patches into 8 habitat clusters, each comprising of 5 closely positioned patches (clustered landscapes). To do this, we first sampled the x- and y-coordinates of 8 patches from a uniform distribution within the limits (0, 1), under the condition that there is a minimum distance of 0.3 between them. Then we closely position 4 patches around each of these 8 patches by drawing their x- and y-coordinates from a truncated normal distribution between 0 and 1 with a mean of $x_{[1,\cdots,8]}$ and $y_{[1,\cdots,8]}$, respectively, and a standard deviation of 0.03. Assigning each landscape different levels of nutrient supply concentrations S_l further allowed us to test the effects of fertilization on invasion success. We applied three nutrient supply scenarios, yielding in total six distinct landscape types: random/clustered-oligotrophic

(S_l = 0.01), random/clustered-mesotrophic (S_l = 1) and random/clustered-eutrophic (S_l = 1000). See Table 1, Eq. T1.8 for further information regarding the nutrient dynamics.

Invasion simulations

We simulated invasions using a three-step process:

1. First, we initialize the native food web by randomly sampling the initial biomass densities $B_{i,z}$ of each species i on any given patch z from a uniform probability density within the intervals (0, 10). To start the simulations with some differences in species composition across patches, we initialize on each patch only 60% of all species from the native web (initial β-diversity), which we draw on each patch at random under the condition that at least one basal species is initialized on each patch, and that the full native web exists in the regional species pool. We further initialize on each patch two nutrients N_l ($l \in 1,2$) of different importance and depending on the nutrient supply scenario, nutrient supply concentrations of S_l = 0.01 (oligotrophic), S_l = 1 (mesotrophic) and S_l = 1000 (eutrophic); holding them constant over all patches.

2. Starting from these random initial conditions, we numerically simulate the feeding and dispersal dynamics of the native meta-food-web for 5.000 time steps using the bioenergetic model formulated in terms of ordinary differential equations described in Section 2 by integrating the system using procedures of the SUNDIALS CVODE solver version 2.7.0 in C++ (backward differentiation formula with absolute and relative error tolerances of 10^{-10}) (Hindmarsh et al. 2005). In short, the rate of change in biomass density of any species i on any patch z, $B_{i,z}$, depends on the difference between its biomass gains due to feeding and immigration, and its biomass losses due to metabolic demands, being preyed upon and emigration. For the equations and parameterization see Table 1 and Table 2.

3. In the third step, at t = 5.000 we introduce the invasive species k on the upper most left patch in the landscape (the 'introduction patch' x, black patch in Figure 1b) by initializing it with a biomass density of $B_{k,x}$ = 5, the mean of the uniform probability density from which we draw the initial biomass densities of the native species. We then continue to compute the dynamics of the now invaded meta-food-web for another 5.000 time steps, using the same parameterization.

In this manner, we simulated for five food webs á 20 species 21 single-species invasions each, each on 20 landscapes and three nutrient supply scenarios. This yielded a total of 6300 simulations. All

code was programmed in C++ and R version 3.5.1 (R Core Team 2019), and simulations were run on a high-performance cluster using a 64-bit platform (Schnicke et al. 2019).

Invader characteristics

In addition to the species traits we used as input parameters (body mass m_k and dispersal range δ_k), we evaluated for each invader k four species-level network properties to describe their typical interaction structure within the native food web at the time of introduction (t = 5.000): The prey-averaged trophic level T_k, i.e., defined as one plus the mean trophic level of all the invader's resource species (Williams and Martinez 2004); the degree of omnivory O_k, expressing the variance in trophic levels of a consumer's prey; generality G_k (prey counts); and vulnerability V_k (predator counts). We calculated T_k (defined as 1 + the weighted average of the trophic levels of its food items) and O_k using the *TrophInd* function of the *NetIndices* package in R version 3.5.1 (Kones et al. 2009, R Core Team 2019). Both G_k and V_k were normalized, respectively, by dividing the number of prey and predator species by the total number of extant species in the meta-food-web at t = 5.000.

Invasion success

An invasion process was counted as successful if an invader k could successfully invade at least one patch in addition to the 'introduction patch' x (on which k was initialized with a biomass density $B_{k,x} = 5$ at t = 5.000). We counted a patch z as successfully invaded if k's biomass density post-simulation at t = 10.000, $B_{k,z}$, exceeded the extinction threshold of 10^{-20}. To quantify an invader's ability to spread across a new environment (invasive spread), we calculated the fraction of successfully invaded patches in a landscape at t = 10.000 (excluding the 'introduction patch'). Additionally, we evaluated the biomass density of an invader in the landscape, B_k, relative to the total biomass density of all species in the landscape, B_t, at t = 10.000.

Analysis and data visualization

We checked for correlation between the initial β-diversity (t = 0) and the β-diversity that emerged by simulating feeding and dispersal dynamics for 10.000 time steps, which was however not the case (see the SI, Figure S5). Further, we removed 1115 simulations for which we could not calculate meaningful trophic levels (animal invaders without prey) and used the remaining 5185 simulations for further analysis. We use boxplots to illustrate the impacts of spatial habitat configuration and nutrient availability on invasion success and the proportion of invader biomass density in a landscape. Boxplots were

generated with the *ggplot2* package in R version 3.5.1 (R Core Team 2019, Wickham 2016), using the default setup. Similarly, we illustrate the impact of each invader trait (body mass, dispersal range) and species-level network property (trophic level, omnivory, generality, vulnerability) on invasive spread, separately for each landscape type. For the purpose of illustration, we combined invasive species into groups, separately for each trait and species-level network property. To do this, we rounded invader body masses, m_k, and degree of omnivory, O_k, up to the nearest multiple of 0.2, dispersal ranges, δ_k, normalized generality, G_k, and vulnerability, V_k, up to one decimal place, and prey-averaged trophic levels, T_k, up to the nearest integer. To illustrate the number of observations in the groups, we draw boxes with widths proportional to the square-roots of the number of observations in each group.

3 Results

Abiotic drivers

Numerically simulating biological invasions in meta-food-webs in landscapes that differ in their spatial configuration of habitat and nutrient supply shows that both landscape properties affect invasion success. In total, approximately 68.5% of all simulated 6300 invasion processes led to successful invasions—counting an invasion as successful if at least one patch in addition to the 'introduction patch' was successfully invaded. We find this fraction to be higher in clustered landscapes (approximately 70.9%) than in random landscapes (approximately 65.7%). Although this applies to all levels of nutrient supply (Figure 2a, dashed line), the differences are more pronounced in oligotrophic and mesotrophic landscapes in which nutrient supply is limited (Figure 2a). Accounting for the spread of an invader across the landscape, we find this pattern to be reversed (Figure 2b). This means in our simulations, invasive species can invade more patches in landscapes in which habitat is randomly distributed than in landscapes in which habitat is clumped into clusters with long distances between them. This applies to all levels of nutrient supply. Considering the invader biomass density relative to the total biomass density in the landscape, we find this fraction to decrease with nutrient supply (Figure 2d)—although the total biomass density in the landscape is increasing with nutrient supply (Figure 2c). This applies both to clustered and random landscapes, showing comparable fractions of total and invader biomass density (Figure 2d). In our simulations, oligotrophic landscapes can in general only support few species at low trophic positions (see the SI, Figure S6), preventing thus also the establishment and further spread of invasive species at higher trophic positions (see the SI, Figure S7, first column). In mesotrophic and eutrophic landscapes with sufficient nutrient supply, invasive species can invade more patches in random landscapes than in

clustered landscapes. Predictably, an increase in nutrient supply facilitated the spread of invasive species even more, particularly so in clustered landscapes (Figure 2b).

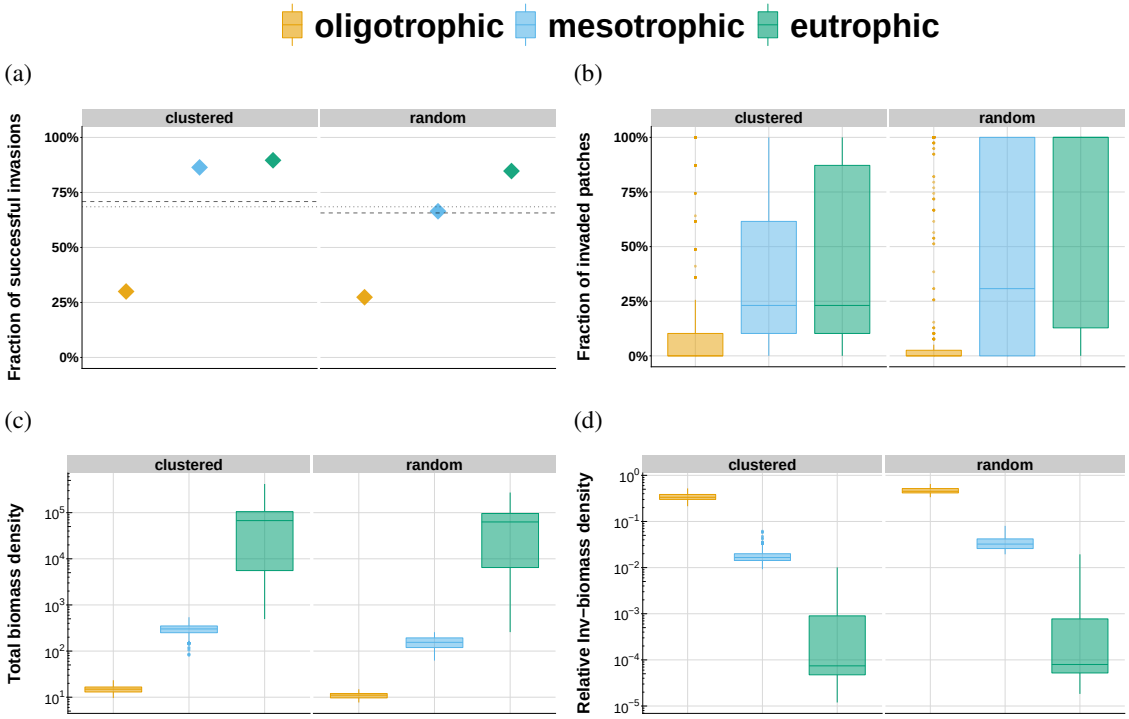


Figure 2: Abiotic drivers. Effects of landscape properties on (a) invasion success (i.e., the invasive species successfully invaded at least one patch in addition to the patch of introduction), (b) the further spread of invasive species across the landscape, (c) the mean total biomass density in a landscape, and (d) the fraction of invader biomass density of the total biomass density in a landscape. Columns indicate the spatial configuration of habitat (clustered and random); colors different levels of nutrient supply. Dashed lines in (a) show the mean invasion success over all levels of nutrient supply for clustered and random landscapes; the dotted line the mean invasion success rate overall landscape types. We evaluated biomass densities, invasion success and invasive species spread post-simulation at time t = 10.0000, and counted a patch as successfully invaded when invader biomass density exceeded the extinction threshold of 10^{-20}. Biomass densities were increased by one and then $\log_{10}$-transformed.

Biotic drivers

Body mass, dispersal ability and trophic level In addition to landscape type and nutrient supply, our simulations show that invasive spread (defined as the spread of an invader across a new environment) varies among invasive species (see the SI, Figure S7). Our results demonstrate that certain species traits and species-level network properties can determine the spread of an invasive species across a new environment (Figure 3), identifying the dispersal range of an invader as the most important predictor for invasive spread. As expected, invaders with large dispersal ranges ('good dispersers') can spread across more patches than invaders with low dispersal ability ('poor dispersers') (Figure 3b). High dispersal ability is especially advantageous in clustered landscapes with long distances between habitat clusters,

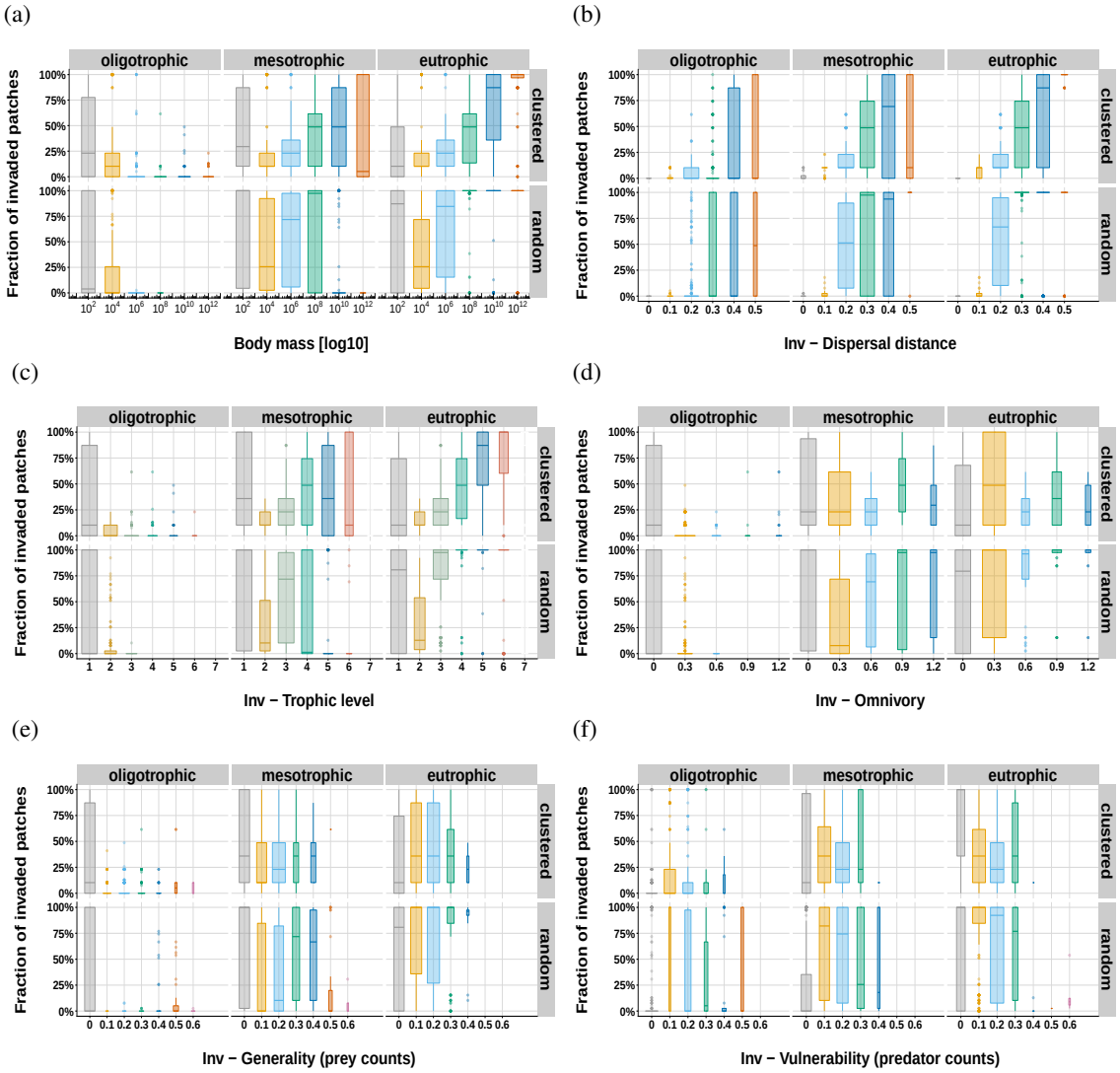


Figure 3: Biotic drivers. Invasive spread (measured as the fraction of invaded patches) in landscapes varying in their spatial configuration of habitat and nutrient availability in response to invasive species traits and species-level network properties: (a) body mass ($\log_{10}$-transformed), (b) dispersal range, (c) prey-averaged trophic level, (d) omnivory index, (e) generality (normalized prey counts) and (f) vulnerability (normalized predator counts). Columns indicate nutrient availability in a landscape; rows the spatial configuration of habitat. Species-level network properties were assessed at the time of introduction (t = 5.000). The fraction of invaded patches was evaluated post-simulation at time t = 10.0000, counting a patch as invaded when the biomass density of the invader exceeded the extinction threshold of 10^{-20}. Box widths are drawn proportional to the square-roots of the number of observations in the groups.

whereas in random landscapes with generally higher invasion success rates the benefits arising from high dispersal ability are less pronounced, in particular under eutrophic nutrient conditions (Figure 3b, third column). In our framework, oligotrophic landscapes (Figure 3, first column) can in general only support few species at low trophic positions (see the SI, Figure S6), preventing thus also the establishment and further spread of invasive species at higher trophic positions (Figure 3a, 3c, first column). Thus, we here focus on mesotrophic and eutrophic landscapes with sufficient nutrient supply (Figure 3, second and third columns respectively), if not explicitly stated otherwise. Besides dispersal ability, the realized trophic level of an invader in the native web at the time of introduction affects its spread across a landscape. In eutrophic landscapes, we find the fraction of invaded patches to increase with trophic level (apart from plant species) (Figure 3c, third column). Whereas in mesotrophic landscapes, animal invaders at higher trophic levels ($T_k > 4$) are limited in their spread, particularly in random landscapes (Figure 3c, second column, second row). For animal species both their dispersal ability and trophic level scale with body mass, and thus, effects of the trophic level might be masked by the increase in dispersal range with trophic level, provided that nutrient availability does suffice to support them. In all landscapes, we find for the spread of plant invaders ($T_k = 1$) with body mass independent dispersal ranges (which we drew at random) a wide range of values (Figure 3c).

Omnivory index, generality and vulnerability The degree of omnivory, O_k, expresses the variance in trophic levels of a consumer's prey ($O_k = 0$ indicates plant species). For animal invaders, we find the fraction of invaded patches to increase with increasing degree of omnivory (Figure 3d, first row). In other words, animal invaders that feed on prey at various trophic levels tend to invade more patches than invaders with a more narrow diet, feeding on species from similar trophic groups. This effect is more pronounced in random than in clustered landscapes, especially under eutrophic conditions (Figure 3d, second row, third column). We find similar trends for invader generality, G_k (normalized prey counts, not accounting for their trophic level) (Figure 3e). The effect of vulnerability, V_k (normalized predator counts), on the fraction of invaded patches also varies among landscape structures and nutrient availability, showing different trends for clustered and random landscapes (Figure 3f). In clustered landscapes, invader vulnerability only marginally affects its invasive spread, whereas in random landscapes, invaders with few predators tend to have an advantage over invaders that are consumed by more native species.

4 Discussion

Invasive species are a major component of global change and pose a severe threat to biodiversity (Courchamp et al. 2017, Ricciardi et al. 2017, Seebens et al. 2017). They can reduce species diversity and population viability and can (permanently) alter ecosystem structure and functioning (Murphy and Romanuk 2014, Mollot et al. 2017). Yet, although they have been subject of intense study for decades (Elton 1958, Lonsdale 1999, Ricciardi et al. 2017, Frost et al. 2019), understanding and accurately predicting invasion success and in particular invasive spread remains a major challenge for ecologists. Biological invasions are complex processes that depend on a large number of interdependent factors acting on a wide range of spatial scales (With 2002, Pantel et al. 2017), including biogeographical landscape properties, abiotic environmental conditions but also species interactions as well as invasive species traits. To account for all relevant factors at both the local and landscape scale we here develop a network-based approach that integrates local and spatial processes of complex food webs in realistic landscapes. The approach is based on a population dynamical meta-food-web model (Ryser et al. 2019) that follows allometric scaling laws for metabolism, feeding and dispersal, allowing us to study what combination of landscape properties underlying food webs and invader properties determine invasion success and in particular invasive spread. Our simulation experiment yields on average approximately 68.5% successful invasion processes, i.e., the invasive species established itself on at least one patch in addition to the patch on which it was introduced. This proportion corresponds closely to the invasion success rates both Hewitt and Huxel (2002) and Romanuk et al. (2009) found in their studies simulating invasions in non-spatial food webs (50-60% and 47%, respectively). Simulating non-spatial food webs, Romanuk et al. (2009) work provides insight how invader traits and native food web properties relate to invasion success (for the latter see also Baiser et al. 2010), whereas Hewitt and Huxel (2002) focus on invasion resistance in (multitrophic) communities depending on the number of invaders (one and two) and initial biomass densities. These studies reinforce the important role of trophic interactions in invasion success, but neglect the spatial context that can impose strong constraints on food web dynamics (Gravel et al. 2016, Ryser et al. 2019). They thus cannot account for factors acting on scales outside the local habitat that can facilitate or prevent invasion success but more importantly invasive spread. However, we know that natural habitats vary in the degree to which they are invaded by exotic species (Williamson and Harrison 2002) and that invasive species may spread more rapidly in fragmented landscapes (Sakai et al. 2001). One historic example, for instance, is the brown-headed cowbird, an avian brood parasite, whose spread accelerated in response to forest clearing (see Sakai et al. 2001 and references therein), highlighting the

importance to jointly consider abiotic and biotic factors as well the underlying landscape properties to advance invasion biology (Mollot et al. 2017).

Clustered landscapes can limit invasive spread

Testing different landscape structures (clustered and random distribution of habitat) and nutrient supply scenarios (oligotrophic, mesotrophic and eutrophic), our simulations yielded different patterns for invasion success (at least one patch in addition to the introduction patch is invaded) and invasive spread (the fraction of invaded patches in a landscape) depending on the spatial habitat configuration and level of nutrient supply. This highlights the important role landscape properties play for the establishment and further spread of invasive species, supported by previous theoretical and empirical studies (see, for example, Sakai et al. 2001, Williamson and Harrison 2002, With 2004, Hastings et al. 2005). In our simulations, in clustered landscapes, long distances between habitat clusters appear to limit the spread of invasive species across the landscape, but very short distances within a cluster seem to facilitate invasions within a cluster. In contrast, randomly distributed habitat generally shows higher fractions of invaded patches, provided there was sufficient nutrient supply. Conforming with our finding that short distances can enhance invasion success and invasive spread, Havel et al. (2002) found that lakes closer to source lakes tended to be more invaded by an exotic water flea than more isolated lakes (based on data collected from 152 Missouri lakes, USA over seven years). In these lake ecosystems, however, they did not find an effect of lake fertility (but see, e.g., Mata et al. 2013), whereas in our simulation experiment, an increase in nutrient supply facilitated invasion success and invasive spread. In our framework, landscapes with high nutrient availability could in general accumulate more biomass, particularly at high trophic levels and thus increase the number of trophic levels a landscape can support, thereby also benefiting invasive species (particularly at high trophic positions). Oligotrophic conditions on the other hand reduced the number of species and trophic levels able to persist, and thus, prevented invasion success and invasive spread due to energy limitation, in particular of species at higher trophic positions (independent of their good dispersal abilities). This suggests that in oligotrophic landscapes invader dispersal ranges and other invader traits are less important than energetic limitations in explaining the strong negative response of higher trophic levels to nutrient deprivation. This is supported by Ryser et al. (2019) who found comparable patterns in their work, showing that habitat isolation induced bottom-up energy limitation can drive top species extinctions in complex meta-food-webs. Interestingly, however, in oligotrophic landscapes we find the highest fractions of invader biomass density relative to the overall biomass density in the landscape. In other words, although oligotrophic landscapes can generally sup-

port only few species at low trophic positions and in general hold less biomass, if successful, an invader makes up a high fraction of biomass in the invaded system. This might indicate that in oligotrophic landscapes invaders could have more severe impacts as they make up a larger proportion of biomass density and species compared to mesotrophic and eutrophic landscapes, provided that they can establish themselves under such restricted conditions.

Invader properties are important

Species traits are key determinants for local and spatial processes, this also applies to biological invasions and invasive spread. In our simulations, invader properties, and in particular dispersal ability, strongly influence the fraction of patches an invader can successfully invade. This supports previous theoretical and empirical studies showing that invader properties are important determinant for invasion success (Sakai et al. 2001, Mata et al. 2013, Mollot et al. 2017), and can be more important than properties of the native community (e.g., the structure of the recipient food web) (Romanuk et al. 2009). In our simulation experiment, we find dispersal ability to be the best predictor for broad-scale invasive spread in fragmented landscapes, followed by trophic level (excluding trophic level 1, i.e., plant species). In our model, we let animal dispersal ability similar to trophic level increase with body mass (active dispersers), whereas for plant species (trophic level 1) we assume passive dispersal and thus body mass independent dispersal ranges that were drawn at random. This means that based on our model setup invaders with good dispersal abilities (which can either be randomly selected plants with long-distance seed dispersal or large animals at high trophic positions with large dispersal ranges) can connect more patches in a landscape (see the SI, Figure S3, giving them an invasion advantage over species with low dispersal abilities. We further find an increase in the fraction of invaded patches with trophic level (except for plant species at trophic level 1). Note however, that based on our model assumptions, both animal dispersal range and trophic level scale with body mass, which is consistent with empirical patterns (Riede et al. 2011, Hein et al. 2012). As a result, animals at high trophic positions can spread further than animals at lower trophic levels, which also applies to animal invader. Therefore, we assume that in our simulations the strong relationship between the invasive spread of animals and trophic level might be mostly attributed to their good dispersal abilities rather than their trophic position. This is further supported by our finding that invasive spread strongly varies among plant invaders at trophic level 1, suggesting that in our simulations dispersal range and not trophic level drive invasive spread (but see Romanuk et al. 2009, Howeth et al. 2016, Hui et al. 2016, showing that trophic position can strongly relate to the invasiveness of a species in non-spatial food webs). Further, body mass and movement

mode but also the spatial configuration of habitat determine which habitat patches a species can connect, i.e., its spatial network (Hirt et al. 2018), pointing towards an interaction between these factors that determine to what extent an invasive species can spread across a new environment. This emphasizes that for a given landscape detailed knowledge of the properties of a potential invader, in our simulations most importantly its dispersal ability, can be extremely valuable to reliable predict and prevent invasive spread (Sakai et al. 2001, Mata et al. 2013). The importance of long-distance dispersal for invasive spread in fragmented landscapes has also been highlighted by With (2004). However, human activities and above all human transport processes, for example, by car, truck or boat greatly facilitate biological invasions and invasive spread, e.g., due to long-distance dispersal of exotic non-native species with high biomasses such as the movement of Argentine ants by cars and trucks, or of zebra mussels by boats (Hastings et al. 2005, Wilson et al. 2009 and references therein). Also, omnivory and generality, both indicating a broad resource variety, can to some extent relate to invasive spread (although less pronounced than dispersal ability and trophic level). Simulating species invasions in non-spatial food webs yielded similar results (Romanuk et al. 2009), suggesting that variables that reflect the interaction between an invader and the invaded community (e.g., trophic position, generality and omnivory) can govern invasion success in complex ecological networks (Romanuk et al. 2009, David et al. 2017). For vulnerability, i.e., the number of species an invader is preyed upon, we find opposite trends, however, these are rather weak. This could indicate that the number of predators an invader is preyed upon is less important in determining its success and spread than having a broad feeding niche, but more importantly, good dispersal abilities.

Model specifications and future directions

Our approach to modelling invasions in meta-food-webs enables the incorporation of species interactions, abiotic environmental conditions and biogeographical landscape properties to explore what determines invasion success and spread in fragmented patchy landscapes. Based on a tested and realistic allometric trophic network model and metacommunity theory our framework is very general. For example, it can be used to study the effects of various additional properties (in terms of landscape, invader and native food web properties) on invasion success and invasive spread but also allows to explore how invaders impact native meta-food-webs. Due to indirect effects present in ecological networks, the invasion of a species can set in motion an entire cascade of subsequent changes. For example, it could lead to an increase or decrease species richness, among others. Furthermore, with all model parameters based on allometric principles, our modelling approach can be simply adapted to other trophic networks

such as empirical food web structures (Brose et al. 2019) or other food web models (Williams and Martinez 2000, Petchey et al. 2008). Also, empirical patch networks or other dispersal mechanisms could be incorporated in the future. Environmental heterogeneity (differences among patches) may influence all stages of the invasion process—introduction, establishment, dispersal, and further spread (reviewed by With 2002). Thus, patch heterogeneity might change the patterns we found. Furthermore, we here introduce each invasive species with a biomass density of $B_k = 5$ at $t = 5.000$, which is compared to the biomass densities of native species at $t = 5.0000$ rather high. This is in line with empirical research showing that invasive species often are introduced with high densities often due to human activities, such as ballast water release (see Hastings et al. 2005, Wilson et al. 2009 and references therein). Although in our simulations initial (invader) biomass densities do not affect the observed patterns (see the SI, Figure S8), introducing invasive species with much lower biomass densities compared to the equilibrium densities of native species might change the results (see, e.g., Hewitt and Huxel 2002). Moreover, if introduced on patches with oscillations, the time of introduction and biomass density might play an important role. Another aspect of our simulations that may affect the generality of our results lies in the way we generate native food webs (see Section 2, *Generating webs*), in which invasive species have a 'free' niche space they can settle into. Also, now we tested only single-species invasions that are introduced once. Future work might involve testing different initial biomass densities at different time steps, as well as waves of invasions, or multi species invasions. Furthermore, most studies taking a (non-spatial) network perspective in invasion biology so far focused on identifying network properties that relate to the 'invasibility' of the resident community and how they are affected by invasive species (Romanuk et al. 2009, Baiser et al. 2010, Frost et al. 2019). The focus of our work was on identifying which combination of landscape properties and invasive species traits and species-level network properties determine invasion success and invasive spread in meta-food-webs, thereby addressing an important but understudied avenue in invasion biology (see Frost et al. 2019).

Synthesis and outlook

Biological invasions are a major component of global change that can cause biodiversity loss and biotic homogenization (Courchamp et al. 2017, Ricciardi et al. 2017). Providing reliable predictors of whether introduced species are able to persist in a new environment and further spread is crucial to improve invasive species management and might also prove valuable for ecological theory. Yet, despite its relevance, our ability to predict which combinations of species, habitats and landscape structures facilitate or prevent biological invasions remains limited. We address this issue, using a holistic network-based

approach that is build on a bioenergetic meta-food-web model and integrates direct and indirect effects arising from local population dynamics and spatial processes. From our simulation experiment the following important conclusions arise: (1) In fragmented landscapes, invader dispersal ability is the best predictor for invasive spread; (2) The differences we find among our simulations emphasize the importance to jointly consider landscape properties (e.g., the distribution of habitat and nutrient availability), species interactions and invader traits; (3) Our results stress the importance of the spatial network structure to predict invasion success and invasive spread, provided there is sufficient nutrient supply in the landscape. More generally, our work shows that it depends on the circumstances when information on network structure should be complemented with invasive species traits to understand invasion success and more importantly, invasive spread. This is highly relevant considering the rapidly progressing land use change and its consequences. Distances between suitable habitat expand and landscapes become increasingly fragmented and isolated (Haddad et al. 2015), comparable to the clustered landscapes we simulated here. Furthermore, land use changes can cause landscape eutrophication, e.g., due to enhanced fertilization, but can also lead to nutrient deprivation. As shown by our results, all these factors can facilitate invasion success and invasive spread in complex systems. However, studies that jointly address abiotic and biotic drivers at scales beyond the local habitat are scarce, although urgently needed. We here provide one promising direction for invasion biology for a better understanding of the interplay between landscape properties, resident communities, and invasive species, which is extremely important to identify potential invaders and mitigate their impacts.

Table 1: Local population dynamics. Equations and model parameters

Animal population dynamics

$$\frac{dA_{i,z}}{dt} = e_P A_{i,z} \sum_j F_{ij,z} + e_A A_{i,z} \sum_k F_{ik,z} - \sum_k A_{k,z} F_{ki,z} - x_i A_{i,z} \tag{T1.1}$$

Rate of change of biomass density of animal species i on patch z; with conversion efficiency $e_P = 0.545$ typical for herbivory (Lang et al. 2017); conversion efficiency $e_A = 0.906$ typical for carnivory (Lang et al. 2017); feeding rate $F_{ij,z}$ of consumer i on resource j on patch z; metabolic demands per unit biomass for animals $x_i = x_A m_i^{-0.305}$ with scaling constant $x_A = 0.141$ (Ehnes et al. 2011, Yodzis and Innes 1992). The first sum goes over all plant resources j, the second over all animal resources k and the third over all animal predators k of animal species i.

Functional response

$$F_{ij,z} = \frac{\omega_i \kappa_{i,j} R_{j,z}^{1+q}}{1 + cA_{i,z} + \omega_i \sum_k \kappa_{ik} h_{ik} R_{k,z}^{1+q}} \cdot \frac{1}{m_i} \tag{T1.2}$$

Per unit biomass feeding rate of consumer i as function of its own biomass density, A_i, (taking interference competition c, which is the time lost due to intraspecific encounters, sampled from a normal distribution with mean $\mu_c = 0.8$ and s.d. $\sigma_c = 0.2$ for each food web), and biomass density of the resource R_j (either animal A_j or plant species P_j); with ϕ_{ij}, resource specific capture coefficient (Eq. T1.3); h_{ij}, resource-specific handling time (Eq. T1.5); $\omega_i = 1/(\text{number of resource species of } i)$, relative consumption rate accounting for the fact that a consumer has to split its consumption if it has more than one resource species.

Capture coefficient

$$\kappa_{ij} = \lambda_l m_i^{\beta_i} m_j^{\beta_j} L_{ij} \tag{T1.3}$$

Table 1: Continued.

Resource specific capture coefficient of consumer species i on resource species j scaling the feeding kernel L_{ij} by a power function of consumer and resource body mass, assuming that the encounter rate between consumer and resource scales with their respective movement speed. We sample the exponents β_i and β_j from normal distributions (mean $\mu_{\beta_i} = 0.42$, s.d. $\sigma_{\beta_i} = 0.05$; $\mu_{\beta_j} = 0.19$, s.d. $\sigma_{\beta_j} = 0.04$, respectively (Hirt et al. 2017b)). We divide here the group of consumer species into the subgroup of carnivorous and herbivorous species each comprising a constant scaling factor for their capture coefficients λ_l with $l \in 0, 1$ ($\lambda_0 = 40$ for carnivorous species and $\lambda_1 = 5000$ for herbivorous species). For plant resources, $m_j^{\beta_j}$ was replaced with the constant value of 1 (as plants do not move).

Feeding efficiency

$$L_{ij} = \left(\frac{m_i}{m_j R_{opt}} e^{1 - \frac{m_i}{m_j R_{opt}}} \right)^{\gamma} \tag{T1.4}$$

Probability of animal i to attack and capture an encountered resource j (which can be either plant or another animal), described by an asymmetrical hump-shaped curve (Ricker's function), with width $\gamma = 2$ centered around an optimal consumer-resource body mass ratio $R_{opt} = 100$, and a maximum of 1. The optimal prey body mass and the location and width of the feeding niche of a predator are parameterized with data from empirical feeding interactions (Brose 2008, Schneider et al. 2016).

$$h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j} \tag{T1.5}$$

The time consumer i needs to kill, ingest and digest resource species j, with scaling constant $h_0 = 0.4$ and allometric exponents η_i and η_j drawn from normal distributions with means $\mu_{\eta_i} = -0.48$ and $\mu_{\eta_j} = -0.66$, and standard deviations $\sigma_{\eta_i} = 0.03$ and $\sigma_{\eta_i} = 0.02$, respectively (Rall et al. 2012).

Table 1: Continued.

Plant population dynamics

$$\frac{dP_{i,z}}{dt} = r_i G_i P_{i,z} - \sum_k A_{k,z} F_{ki,z} - x_i P_{i,z} \tag{T1.6}$$

Rate of change of biomass density of plant species i on patch z; with predation loss $F_{ki,z}$ summed over all consumer species k feeding on plant species i; metabolic demands per unit biomass for plants $x_i = x_P m_i^{-0.25}$ with $x_P = 0.138$; intrinsic growth rate $r_i = m_i^{-0.25}$; species specific growth factor G_i (Eq. T1.7).

Growth factor

$$G_i = min\left(\frac{N_1}{K_{i,1} + N_1}, \frac{N_2}{K_{i,2} + N_2}\right) \tag{T1.7}$$

Species-specific growth factor of plants determined dynamically by the most limiting nutrient $l \in 1,2$; with $K_{i,l}$, half-saturation densities determining the nutrient uptake efficiency assigned randomly for each plant species i and nutrient l (uniform distribution within (0.1, 0.2)). The term in the minimum operator approaches 1 for high nutrient concentrations.

Nutrient dynamics

$$\frac{dN_{l,z}}{dt} = D(S_l - N_l) - \nu_l \sum_{i,z} r_i G_i P_{i,z} \tag{T1.8}$$

Rate of change of nutrient concentration N_l of nutrient $l \in \{1,2\}$ on patch z, with global turnover rate $D = 0.25$, determining the rate at which nutrients are refreshed; supply concentration S_l, determining the maximum nutrient level of each nutrient, l (oligotrophic: $S_l = 0.01$, mesotrophic: $S_l = 1$, eutrophic: $S_l = 1000$); relative nutrient content in plant species biomass ν_l ($\nu_1 = 1$, $\nu_2 = 0.5$).

Table 2: Dispersal dynamics. Equations and model parameters

Emigration rate

$$E_{i,z} = d_{i,z} B_{i,z} \tag{T2.1}$$

Emigration rate of species i from patch z, where $d_{i,z}$ is the per capita dispersal rate of species i on patch z, and $B_{i,z}$ is the total biomass density of species i on patch z (Eq. T2.2).

Per captia dispersal rate

$$d_{i,z} = \frac{a}{1 + e^{b(x_i - \upsilon_{i,z})}} \tag{T2.2}$$

The per capita dispersal rate of species i on patch z, with $a = 0.1$ is the maximum dispersal rate, $b = 10$, a parameter determining the shape of the function, x_i, the inflection point determined by the metabolic demands per unit biomass of species i, and $\upsilon_{i,z}$, the per capita net growth rate accounting for emigration triggers such as resource availability, predation pressure and inter- and intraspecific competition (Bowler and Benton 2005, Fronhofer et al. 2018). This means if a species' net growth rate is positive, there is no need for dispersal and emigration will be low; but if the local environmental conditions deteriorate, the growing incentives to 'search' for better habitat increase the fraction of emigrating individuals (see SI, Figure S4).

Maximum dispersal distance (animals)

$$\delta_i = \delta_0 m_i^{\epsilon} \tag{T2.3}$$

Table 2: Continued.

Maximum dispersal distance of animal species i, with body mass m_i, scaling exponent $\epsilon = 0.05$, determining the slope of the body mass scaling (the positive value accounts for a higher mobility of animals with larger body masses), and intercept δ_0. We set $\delta_0 = 0.1256$ so that the largest possible animal species with a body mass of $m_i = 10^{12}$ has a maximum dispersal range of $\delta_i = 0.5$ (half of the edge length of the landscape). An animal species with the smallest possible body mass of $m_i = 10^2$ thus has a maximum dispersal range of $\delta_i = 0.158$.

Immigration rate

$$I_{i,z} = \sum_{n \in N_z} E_{i,n}(1-\delta_{i,nz}) \frac{1-\delta_{i,nz}}{\sum_{m \in N_n} 1-\delta_{i,nm}} \tag{T2.4}$$

Immigration rate of species i into patch z, where N_z and N_n are the sets of all patches within the dispersal range of species i on patches z and n, respectively, $E_{i,n}$ is the emigration rate of species i from patch n, the term $(1-\delta_{i,nz})$ is the fraction of successfully dispersing biomass, i.e., the fraction of biomass not lost to the matrix, and $\delta_{i,nz}$ is the distance between patches n and z relative to species i's maximum dispersal distance δ_i. The term $\frac{1-\delta_{i,nz}}{\sum 1-\delta_{i,nm}}$ determines the fraction of biomass of species i emigrating from source patch n towards target patch z and depends on the relative distance between the patches, $\delta_{i,nz}$, and the relative distances to all other potential target patches m of species i on the source patch n, $\delta_{i,nm}$. This means more biomass flows between patches with small distances.

Data and code availability: Code to reproduce numerical results and figures will be provided upon acceptance.

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III

General Discussion

1 | Synopsis

Natural ecosystems are faced with constantly varying environmental conditions and whether a population or a community can persist depends on its ability to cope with these changes. As discussed in detail in the introduction, most environmental pressures on ecosystems are exerted by us humans and our rising demand for natural resources (IPBES, 2019). As a result, biodiversity on Earth is rapidly disappearing (Pimm et al., 1995; Barnosky et al., 2011; Ceballos et al., 2015, 2017). Nevertheless, predicting the impacts of human activities like land use changes on populations, communities, and especially complex ecosystems remains one of the biggest challenges ecologists are faced with today. Accurate predictions require a clear mechanistic understanding of the underlying, ecological processes in realistically complex ecosystems, like species interactions and dispersal dynamics in food webs. Such an understanding is lacking, because in food webs aspects of spatial scale have been largely overlooked, thus we have limited evidence evaluating how trophic interactions and dispersal processes affect the robustness of multitrophic metacommunities to global changes at broader spatial scales (see the reviews by Pimm and Raven, 2000; Holt, 2002; Amarasekare, 2008; Hagen et al., 2012). Studies investigating global change impacts in complex food webs across habitat boundaries therefore are urgently needed if we want to grasp the scale of global change impacts on realistically complex ecosystems.

In this thesis I addressed this issue by analyzing food webs in a metacommunity context to investigate the causes and consequences of global change on meta-food-webs. My research ambition was driven by the following questions: What are the ecological impacts of global change on meta-food-webs at different levels of biological organization and spatial scale? What happens when the balance in a meta-food-web is disturbed, for instance, due to land use changes, and why do some species and trophic groups react more sensitively to these changes and thus might be more likely to go extinct? To answer these questions, I developed new theoretical frameworks for studying realistically complex meta-food-webs, both in terms of their trophic interactions and their dispersal dynamics. This enabled me firstly, to delve into the underlying mechanisms governing the impacts of global change on meta-food-webs in complex landscapes, and secondly, to explore the variability of these responses among species, trophic groups, landscapes and environmental stressors.

2 | Discussion

Human land use is fragmenting landscapes, limiting the dispersal of organisms between habitats (Haddad et al., 2015) but we lack knowledge of the interplay with trophic interactions. Land use change

impacts on species interactions have been of considerable interest with a few studies also assessing these impacts across a range of trophic levels (e.g., Pace et al., 1999; Binzer et al., 2012; Tylianakis and Binzer, 2014; Binzer et al., 2016; Liao et al., 2017a,b). Nevertheless, systematic explorations that address global change impacts across a large range of trophic levels and spatial scales are scarce (Gonzalez et al., 2011), and for multitrophic metacommunities in complex landscapes virtually absent (but see McWilliams et al., 2019). In research chapters 1 and 2, I filled this scientific gap by testing how land use changes that altered the spatial habitat configuration affected species extinction rates and diversity patterns in meta-food-webs (the latter only in research chapter 1) at different levels of biological organization and spatial scales. I showed for the first time that meta-food-web responses to habitat loss and habitat fragmentation are mediated by an interplay of biotic (species interactions and dispersal) and abiotic factors (spatial habitat configuration). This interplay between species and their environments triggered species extinctions and diversity declines when landscapes became increasingly isolated, with especially devastating effects for species at high trophic levels. This coincides with the trophic rank hypothesis and corresponds to the patterns found by Liao et al. (2017a,b) for tritrophic food chains in fragmented landscapes.

Although species interactions and trophic level have been shown to be important factors determining species' responses to land use changes in previous studies (for example, Van Nouhuys, 2005; Tylianakis et al., 2008; Tylianakis and Binzer, 2014; Liao et al., 2017a,b,c), it remained unclear whether similar trends would also emerge in realistically complex ecosystems like meta-food-webs. The results presented in research chapters 1 and 2 show, for the first time, that these patterns also hold true for meta-food-webs with species across multiple trophic levels dispersing between multiple habitat patches. In both research chapters, top species had elevated extinction risks if habitat became increasingly isolated despite their implied superior dispersal abilities and thus higher landscape connectivity. The elevated extinction risk of top species in response to habitat isolation was consistent across both research chapters. This consistency underpins the generality of this finding, as it emerged, although I used two different modelling approaches, tested different model parameterizations (foremost in research chapter 2), and addressed the effects of habitat isolation in two different ways. While in research chapter 1, I compared increasingly fragmented landscapes that differed in their degree of habitat isolation and the number of habitat patches, in research chapter 2, I simulated progressive habitat loss by gradually removing habitat patches from the landscape.

In research chapter 1, I used a bioenergetic and explicit population dynamical meta-food-web model that allows for great biological realism by defining direct (predation) and indirect (facilitation, competition) effects among species. Like much of current food web theory this model follows

allometric scaling laws for metabolism, growth and feeding (Yodzis and Innes, 1992; Brose et al., 2006a; Schneider et al., 2016) and is combined with an allometric spatial network model (Hirt et al., 2018) to describe the effect of the allometric scaling of dispersal distance on the realized connections between habitat patches (i.e., species-specific spatial networks). In this framework, I attributed the elevated extinction risk of species at high trophic positions (i.e., large-bodied top predators) to the energy limitations that arose when landscapes became increasingly isolated. Although consistent with previous studies showing the elevated extinction risks of top species in fragmented landscapes (Van Nouhuys, 2005; Liao et al., 2017a,b), in contrast to our expectations, their superior dispersal abilities enabling them to connect fragmented landscapes better could not compensate for the bottom-up energy limitation in highly isolated landscapes. This can, in part, be attributed to the inefficient transport of energy between species and trophic levels (in natural systems the transfer efficiency is often only around 10% (Lindeman, 1942)) but to a large part also to the high dispersal losses large-bodied top predators suffered during traversing through the hostile habitat matrix (we did not allow for feeding to take place in the matrix). In combination, these two processes drove top species quickly towards extinction if landscapes became highly isolated as the available energy in the system did not suffice to meet their high energetic demands. In natural systems these patterns could be further elevated as energy availability decreases with trophic level and thus natural systems often are characterized by a pyramidal structure of biomass across the trophic levels of a food web because of the aforementioned inefficient transport of energy between species and trophic levels (Elton, 1927; Lindeman, 1942). This pyramidal distribution of biomass might further amplify the risk for top species extinctions in systems in which energy is limited (Post, 2002; Takimoto and Post, 2013). Moreover, this research chapter demonstrates that environmental changes (here habitat isolation) not only drive species extinct but also affect biomass distributions, community composition and thereby may also cause the loss and/or reorganization of species interactions (see also Tylianakis et al., 2008; Tylianakis and Binzer, 2014; Valiente-Banuet et al., 2015; Binzer et al., 2016). This can lead to vast shifts in the stability and functioning of ecosystems by reducing species diversity and trophic complexity (Brose and Hillebrand, 2016).

In highly fragmented landscapes, dispersal ability of species is an important driver of community dynamics (Pacala and Levin, 1997; Loreau and Mouquet, 1999; Kneitel and Miller, 2003; Thompson et al., 2017). Dispersal is generally assumed to be beneficial for population and community persistence, especially in fragmented patchy landscapes (see, for example, Hanski, 1998; Leibold et al., 2004; Holyoak et al., 2005). However, as shown here, there are also costs associated with dispersal (see also Bonte et al., 2012). This is especially relevant in human-modified landscapes, as land use changes can

heighten the stress and mortality during dispersal. For example, by decreasing the quality of the habit matrix, thus dispersal success might be drastically reduced, thereby accelerating species extinctions (as shown in research chapter 1). This shows that maintaining a suitable habitat matrix in human-modified landscapes can be crucial for species persistence by enhancing landscape connectivity and minimizing dispersal losses, as shown also by Debinski and Holt (2000), Prugh et al. (2008), and Franklin and Lindenmayer (2009). This is an important result given the centrality of this issue for developing effective conservation efforts and shows that improving the quality of the habitat matrix and enabling species to connect isolated habitats (e.g., by constructing wildlife crossings) can facilitate high conservation returns (Taylor and Goldingay, 2010; Reck et al., 2019). Furthermore, the crucial role of successful dispersal for species persistence is also in accordance with classic patch occupancy models, first proposed by Levins (1969), which assume infinitely many patches of suitable habitat, all mutually reachable from any other. These models highlighted that persistence is achieved when the colonization rate exceeds the extinction rate (Levins, 1969), a characteristic that is also common to more complex metapopulation and metacommunity models (e.g., Hanski and Ovaskainen, 2000; Grilli et al., 2015).

Summarizing the above, it can be said that in research chapter 1, habitat isolation deconstructed meta-food-webs from top to bottom trough the combined effect of bottom-up energy limitation and high dispersal losses, with devastating impacts on their trophic complexity. This emphasizes the importance to consider real-world complexity at the food web and the landscape scale when assessing species responses to landscape changes. Following this discovery, however, I realized that much of these processes might have been driven by the underlying biological assumptions and the choice of model parameters (majorly based on (recent) empirical data, see Table B.S2 in the corresponding Supplementary Information, Appendix B). Although explicitly simulating feeding and dispersal dynamics allows for great biological realism and allowed me to elucidate the direct and indirect mechanisms responsible for top species extinctions in response to habitat isolation, I was also restricted in network sizes that were computationally feasible, both in terms of food webs and landscapes. Natural food webs, however, can comprise of hundreds or even thousands of species (Brose et al., 2019) distributed across hundreds of patches. To efficiently explore much larger systems, in research chapter 2, I developed another method to study multitrophic metacommunities: a Bayesian network approach to trophic metacommunities. In this approach, I combined classic metapopulation theory (Hanski, 1998; Ovaskainen and Hanski, 2001) and Bayesian network representations of food webs (Eklöf et al., 2013). With this method I tested the effects of progressive habitat loss, applying three habitat loss scenarios on meta-food-webs with 400 species in landscapes with 300 patches. The habitat

loss scenarios varied in the order in which I removed habitat patches from the landscape, depending on their value for the persistence of the metacommunity as a whole. As discussed before, also here was valid that top species went extinct first with progressing habitat loss (see also Dobson et al., 2006). The extinction rates of top species and species in general, however, strongly depended on the order in which habitat was lost from the landscape. Removing habitat patches of low value to the persistence of the metacommunity as a whole strongly decreased the likelihood of species going extinct, especially so for top species; whereas removing patches of high value first or randomly led to a quick collapse of the metacommunities from top to bottom, as shown also in research chapter 1. Perhaps most strikingly, I found nearly indistinguishable effects on extinction rates if patches were removed at random or high value patches were prioritized (worst-case scenario). This similarity let met to explore the emerging habitat distributions. In both the worst-case and the random scenario, the removal of habitat patches resulted in highly fragmented landscapes with habitat scattered across the landscape. In contrast, removing low value patches resulted in landscapes with a clumped distribution of habitat in which metacommunities could tolerate the loss of more than 90% of the patches. Finding this strong difference between the scenarios or the absence thereof, clearly emphasizes the importance of high landscape connectivity for maintaining trophic complex metacommunities, as shown also in research chapter 1. This emphasizes again that land use changes that reduce landscape connectivity, thereby restricting successful dispersal between local communities, can accelerate (top) species extinctions, as shown also by Gravel et al. (2016), Horváth et al. (2019), and McWilliams et al. (2019). The latter, for example, studied the effects of contiguous and random habitat loss on the stability of multitrophic 'hybrid' communities (i.e., communities combining mutualistic and antagonsitic interactions) with an individual-based approach. In accordance with our findings, McWilliams et al. (2019) showed that community responses to habitat loss majorly depend on the spatial configuration of habitat, and the imposed constraints on individuals' mobility. Therefore, conservation efforts should focus on maintaining high landscape connectivity (but see Gonzalez et al., 2017). This may be achieved by identifying and conserving high-value habitat clusters to enhance multispecies persistence and to maintain trophic complexity (Duffy, 2003; Solé and Montoya, 2006; Hagen et al., 2012).

In addition, testing the Bayesian metacommunity framework in a case study, the plant-mammal Serengeti food web dataset (Baskerville et al., 2011), has proven that it can be readily applied to empirical systems. This dataset, however, did not include a spatial dimension and to my knowledge, data encompassing realistically complex landscapes and food webs is not available so far. Filling this data gap is of urgent need to test and validate the predictions derived from meta-food-web models

with empirical observations, thus future research should work towards a synthesis between empirical and theoretical ecology (Ives and Agrawal, 2005).

Focusing on the effects of land use changes that alter the spatial configuration of habitat in research chapters 1 and 2, I have demonstrated that to understand and predict global change impacts in meta-food-webs it is important to study the interplay of abiotic (landscape structure) and biotic factors (species interactions and dispersal). Yet, as discussed in the introduction, global change drivers most often do not act alone but rather collectively threaten biodiversity (Bowler et al., 2020). For instance, as shown by Didham et al. (2007), habitat loss can facilitate biological invasions in human-modified landscapes. In research chapter 3, I therefore investigated the joint effects of invasive alien species and land use changes in meta-food-webs. To achieve this, I developed a holistic-network based approach that employs single-species invasions by animal and plant species on the basis of the allometric population dynamical meta-food-web model from research chapter 1, thus offering detailed insights into the invasion processes in meta-food-webs. Building on the importance of the spatial configuration of habitat for species persistence and meta-food-dynamics I found in research chapters 1 and 2, I specifically explored if and how habitat configuration (clustered and random distribution of habitat) in combination with fertilization (level of nutrient supply) and invasive species traits (e.g., body mass, dispersal ability, trophic position, and diet breadth) can facilitate or prevent invasions and invasive spread in meta-food-webs. Using this setup, I could show that the spatial configuration of habitat in concert with the environmental conditions and the dispersal ability of the invader determined invasion success. While long distances between habitat clusters could minimize the spread of an invader across the landscape (compared to landscapes with random distribution of habitat), very short distances within a habitat cluster initially facilitated their successful establishment. Furthermore, as eutrophic landscapes with higher energy availability could in general support communities of higher trophic complexity than oligotrophic landscapes, eutrophic conditions also benefited the establishment and spread of invasive alien species, especially ones at high trophic positions with good dispersal abilities. This is in support to the energy limitation I discussed in the context of top species extinctions in research chapter 1. It further illustrates that although high productivity can to some extent stabilize ecological networks by increasing the persistence of species across multiple trophic levels (Takimoto and Post, 2013), such conditions also can facilitate biological invasions (see also Vieira et al., 2017). Furthermore, eutrophic conditions could also lead to the dominance of native species that are strong competitors (Tilman, 1985). By contrast, under oligotrophic conditions alien species could often not establish, but if successful they made up a higher amount of species and biomass in the invaded community, and thus, might entail more devastating impacts for the native community

(Stachowicz et al., 1999). With nutrient pollution and heavy fertilizer input common in agricultural landscapes in combination with changes in the spatial configuration of habitat (e.g., due to habitat loss and fragmentation), such landscape features of human-modified landscapes might further promote biological invasions, as shown for example by Ficetola et al. (2010) and Murphy and Romanuk (2014). In support of this, in a recent macroecological approach that mapped the anthropogenic drivers of biodiversity change, Bowler et al. (2020) showed that global change drivers commonly do not act alone and that more research should address the joint impacts of multiple global change drivers and their interactive effects on biological communities. Based on their findings they conclude that identifying which drivers commonly overlap under which environmental conditions is crucial to develop conservation strategies that simultaneously address multiple aspects of environmental change as they are likely to be more efficient in the long-term (see Bowler et al., 2020 and references therein).

Surprisingly, invasive species have only rarely been addressed in the context of complex food webs (but see Romanuk et al., 2009; Baiser et al., 2010; Lurgi et al., 2014; Ricciardi et al., 2017; Frost et al., 2019; Hui and Richardson, 2019) and studies analyzing biological invasions in meta-food-webs are to my knowledge virtually absent. As shown here, taking into account the entire complexity of food webs and the landscape context allows for better identification of the properties of invasive species, food webs, and landscapes to understand the ecological mechanisms underlying successful invasions. In particular, I found invasive species traits to be important predictors for invasion success, above all, dispersal ability and diet breadth, as shown also by Mata et al. (2013) and Lurgi et al. (2014). These traits are also common to species that can better tolerate land use changes (e.g., Öckinger et al. (2010) showed that species with low mobility, a narrow feeding niche and low reproduction suffered most from habitat loss). These findings again imply that human-modified landscapes can promote biological invasions as successful invaders are often good dispersers and habitat and trophic generalists, and thus also might be more tolerant towards lands use changes and fragmentation effects. This clearly demonstrates that land use changes and invasive alien species interact with each other and can have synergistic effects (see also Benning et al., 2002; Didham et al., 2007; Brook et al., 2008; Mata et al., 2013; Lurgi et al., 2014). The strength of these effects can strongly determine how natural ecosystems respond to these environmental changes. Overall, the results presented in research chapter 3 clearly demonstrate that in combination with landscape features and invader traits, food web structures and dynamics act as an important biotic filter determining the invasion potential of a landscape. As such, this chapter contributes to a better understanding of the interacting effects of abiotic and biotic factors determining biological invasions in complex human-dominated ecosystems.

This is highly important in the face of accelerating invasion rates and can be used to inform invasive species management and restoration.

3 | Challenges and outlook

The findings presented in this thesis majorly assume dispersal ranges increase with trophic level based on the assumption that top species with larger body masses have higher movement capacities and thus can disperse further (Hirt et al., 2017a; Hirt et al., 2018). Although this implication is consistent with previous theoretical frameworks and empirical observations (Jenkins et al., 2007; Holt, 2002; Hirt et al., 2018), dispersal distances and rates may not always increase with trophic level; in some ecosystems they might actually decrease (Beisner et al., 2006; Pedersen et al., 2016; Villarino et al., 2018). For example, Villarino et al. (2018) found a negative relationship between body size and the estimated dispersal scales for different plankton communities; dispersal scale was rather determined by local abundance (which in turn scales with body size) (Villarino et al., 2018). Similar patterns have been shown before for zooplankton and fish in lake systems (Beisner et al., 2006). Larger species at high trophic positions dispersed more rarely than smaller organisms, which Beisner et al. (2006) attributed to community dissimilarity patterns. Furthermore, it can be argued that host-parasitoid networks in agricultural systems do not fit the higher trophic level, higher dispersal framework (unless the parasitoid adults are considered that do disperse which then leads to a population dynamics issue) (Cronin and Reeve, 2005; Van Nouhuys, 2005; Elzinga et al., 2007).

Also, the food web models used in research chapters 1 and 3 are based on allometric principles for metabolism, growth, feeding and dispersal. Body mass is an important predictor for other species traits (Brown et al., 2004; Savage et al., 2004), species interactions (Brose et al., 2005; Woodward et al., 2005; Brose et al., 2006a; Rall et al., 2012; Brose et al., 2019) as well as dispersal processes (Hirt et al., 2017a; Hirt et al., 2018), with strong impacts across ecological scales. Although the use of allometric scaling principles has simplified model parameterization significantly (Hudson and Reuman, 2013), there are important effects independent of body mass that drive biological rates (Brown et al., 2004), species interactions and community structure (Petchey et al., 2008; Boukal, 2014; Jonsson et al., 2018). For example, temperature controls individual biological rates (Brown et al., 2004) and species interactions (Rall et al., 2012). Furthermore, in a recent study, Jonsson et al. (2018) emphasize that although in simple food web modules body mass is an important predictor for the interaction strengths between species, its predictive power decreases with trophic complexity. The authors name several traits other than body mass that have been shown to impact feeding interactions, such as hunting mode (see also

Brose-Hirt, 2018), microhabitat use, aggressiveness of predators, defense strategies of prey species, and predator-induced changes in prey behavior, physiology and/or morphology (Jonsson et al., 2018 and references therein). Similarly, by analyzing how species traits constrain the architecture of complex natural food webs from various ecosystems, Brose et al. (2019) could show that the inclusion of other predator traits (foremost their metabolic and movement types) yielded more accurate predictions of which species are engaged in high body-mass ratio predator-prey interactions.

Taken together, this indicates that an important outcome of collective dynamics in natural ecosystems depends on how species traits in addition to body mass influence the organization of complex ecological networks across habitat boundaries. Nonetheless, allometric (meta-)food web models have been shown to constitute an important tool to explore effects of community assembly, food web structure, dynamics and stability as well as ecosystem functioning driven by trophic interactions (and dispersal dynamics). To improve their predictive power with increasing trophic and landscape complexity, future work should focus on advancing our knowledge of the allometric scaling constants, especially for dispersal processes, and address how their values may vary among organisms, communities, and landscapes. One avenue to achieve this is to identify and incorporate further species traits to improve our predictions of feeding (Brose-Hirt, 2018; Jonsson et al., 2018; Brose et al., 2019) and dispersal links (Hirt et al., 2018) and to include factors such as density- and behavior-mediated effects (Beisner et al., 2006; Eklöf et al., 2012; Årevall et al., 2018; Villarino et al., 2018).

A core assumption of the Bayesian network approach to trophic metacommunities I used in research chapter 2 is that extinction risks only depend on bottom up effects, as species' dynamics are solely dependent upon the persistence probabilities of their prey, but not their predators. In natural ecosystems, however, resources may respond to the loss of their consumers and therefore, extinctions and community changes can be caused by top down effects and top predator loss or declines (see, for example, Terborgh et al., 2001; Borrvall and Ebenman, 2006; Heithaus et al., 2008; Estes et al., 2011). So far, there is no accurate guidance on when top down effects are expected to be important, and thus, integrating the presence of potential top down effects highlights a key area of future research within this method.

Furthermore, in this thesis I assumed homogeneous landscapes in which all habitat patches share the same abiotic conditions. However, in research chapter 3, I demonstrated that altering the environmental conditions of a landscape in terms of their nutrient supply strongly affected meta-food-web dynamics and stability. In addition to these differences at the landscape scale, in real landscapes, especially in human-modified ones such as agricultural areas, habitats are often highly heterogeneous.

This means some habitats may be more suitable to (some) species than others, for example, due to higher quality, thus ensuring greater fitness in terms of persistence, reproduction and dispersal. These differences in habitat quality could foster source sink dynamics (Dunning et al., 1992; Mouquet and Loreau, 2003; Gravel et al., 2010), promote biodiversity through rescue and drainage effects (Ryser et al., in revision) but also destabilize food webs (Gounand et al., 2014). Moreover, landscapes are dynamic, thus the distribution of suitable habitat may vary over space and time. This spatio-temporal variation in the distribution of habitat availability in landscapes may also affect species persistence, as shown, for instance, by Van Teeffelen et al. (2012). Despite the importance of these aspects, they were beyond the realms of this thesis, offering important avenues for future explorations.

In addition, climate change (and in particular warming) is a key component of global change that has been shown to affect individuals, species interactions, interaction strength and food webs (Tylianakis et al., 2008; Brose et al., 2012; Binzer et al., 2012, 2016; Gibert, 2019), as well as movement, dispersal processes and landscapes (O'Connor et al., 2007; Altermatt et al., 2008; Eklöf et al., 2012; Barnes et al., 2015; Gibert et al., 2016; Holyoak and Heath, 2016). Similar to the patterns I presented for land use changes showing the higher vulnerability of top species to habitat isolation, higher trophic levels have been shown to be more sensitive towards climate change (see Gilman et al., 2010 and references therein). Considering that climate change and land use changes occur simultaneously (Brook et al., 2008; Bowler et al., 2020), their combined effects might further accelerate top species extinctions trough various mechanisms acting at the individual, community and ecosystem scale (see, for example, Benning et al., 2002; Northrup et al., 2019).

In this thesis I focused on antagonistic feeding interactions within food webs (who eats whom), but natural ecosystems are composed of complex ecological networks of species interacting in different ways (e.g., mutualistic interactions like in plant-pollinator networks and other types of antagonistic interactions, such as host-parasitoid networks) (Kéfi et al., 2012, 2016; McWilliams et al., 2019; Hale et al., 2020). Different types of interactions and networks vary in their response to different aspects of global change. In two recent reviews, Tylianakis and Morris (2017) and Frost et al. (2019) discuss these differences in detail for environmental changes in various types of ecological networks, including food webs and plant-pollinator networks (Frost et al., 2019 only for biological invasions). These differences emphasize the importance to synthesize different types of ecological networks (so called multiplex networks) to better understand the effects of global change on real ecosystems at the species, landscape, and ecosystem level. Taking into account the multiplex structure of metacommunities will be crucial for determining how global change will impact biodiversity across habitat boundaries.

Addressing these challenges calls for more studies that bridge disciplinary gaps to advance our understanding of global change impacts on natural ecosystems and species extinction rates.

4 | Synthesis

Predicting the impacts of different global change drivers on realistically complex ecosystems like meta-food-webs is a major challenge. Predictions routinely have focused on the direct effects of global change on individual species but as shown in this thesis, interactions between species and between species and their environment strongly influence how global change affects organisms at every scale by altering the structure and dynamics of their community and environment. Neglecting these interactions and their underlying mechanisms can significantly limit the ability to predict responses of species to global change.

To unravel the causes and consequences of changes in meta-food-webs in complex landscapes, and their underlying, ecological mechanisms, this thesis proposes new models that for the first time encompass real-world complexity for two key ecological processes: trophic interactions and dispersal. Compared to the models used in earlier studies (see the introduction and the former sections), the models presented here are more trophically complex and therefore elucidated how species interactions and dispersal shape realistic food web responses to global changes. This demonstrates that to accurately predict global change impacts requires holistic methods that span organism sizes, trophic levels, and habitat boundaries. I accomplish this by combining broad areas of ecological theory: food web ecology, metabolic theory, metapopulation/metacommunity theory, as well as landscape and global change ecology. Thereby, this thesis aligns multidisciplinary research to common goals and perspectives and as such, presents a major step towards a clearer mechanistic understanding of how complex ecosystems respond to global changes.

To summarize, the main achievements of this thesis are the following: Firstly, it proposes models of multitrophic metacommunities dispersing in fragmented landscapes. Secondly, it identifies the interacting processes of trophic and spatial dynamics that in combination with landscape features (habitat configuration and environmental conditions) shape the ecological responses of complex ecosystems to environmental stressors. Thirdly, it provides mechanistic explanations how land use changes can dramatically alter the composition of realistically complex meta-food-webs due to the increased sensitivity of higher trophic levels towards these changes. Thereby, it clearly emphasizes the importance of maintaining high landscape connectivity (e.g, by conserving habitat clusters and improving the quality of the habitat matrix) for preserving species-rich and trophically

complex communities. Together, these findings underpin previous theoretical studies and empirical observations by accounting for the first time for real-world complexity at the food web and the landscape scale. These important insights for community ecology and conservation would not have been revealed without the presented analyses of complex communities at different levels of biological organization and spatial scales. They emphasize the need for similar networks-on-networks approaches to elucidate generalized patterns in ecosystem responses to global change. Thereby, this thesis highlights key areas for future theoretical explorations and empirical research and provides important contributions to better predict and manage biodiversity change in natural ecosystems.

A

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B

Supplementary Information for Research Chapter 1

Remo Ryser, Johanna Häussler, Markus Stark, Ulrich Brose, Björn C. Rall & Christian Guill. 2019. ”The biggest losers: habitat isolation deconstructs complex food webs from top to bottom”. Proceedings of the Royal Society B 286: 20191177.

B.S1 Food web and local population dynamics

We consider a multitrophic metacommunity consisting of 40 species on a varying number of randomly positioned habitat patches, Z (the meta-food-web, figure II.1b). All patches have the same abiotic conditions and each patch can potentially harbour the full food web, consisting of 10 basal plant and 30 animal consumer species. The feeding links (i.e. who eats whom) are constant over all patches (figure II.1a,b) and are as well as the feeding dynamics determined by the allometric food web model by Schneider et al. (2016). We integrate dispersal as species-specific biomass flow between habitat patches (figure II.1b,d).

Using ordinary differential equations to describe the feeding and dispersal dynamics, the rate of change in biomass density, $B_{i,z}$, of species i on patch z is given by

$$\frac{dB_{i,z}}{dt} = T_{i,z} - E_{i,z} + I_{i,z}\,, \tag{B.1}$$

with $T_{i,z} = v_{i,z} \cdot B_{i,z}$ as the rate of change in biomass density determined by local feeding interactions (where $v_{i,z}$ is the per capita growth rate), $E_{i,z}$ as the total emigration rate of species i from patch z (equation B.2), and $I_{i,z}$ as the total rate of immigration of species i into patch z (equation B.4).

B.S1.1 Local food web dynamics

We use an allometric trophic network model (ATN model) based on the work of Schneider et al. (2016) & Kalinkat et al. (2013) to simulate the trophic dynamics of local populations ($T_{i,z}$ in equation B.1). Regarding this term, we distinguish between animal species (Equation T1-1) and basal plant species (Equation T1-6). In each patch, the biomass dynamics of animal species (biomass densities $A_{i,z}$) is given by the differences between growth due to consumption of animal or plant species and losses due to mortality through predation and metabolic demands. The rate of change in plant biomass densities, $P_{i,z}$, depends on the uptake of the two resources, mortality through grazing, and also accounts for metabolic losses. We used a dynamic nutrient model (equation T1-8) with two nutrients (concentrations $N_{l,z}$) of different importance as the energetic basis of our food web (Brose, 2008; Schneider et al., 2016).

The topological network model is an extension of the niche model originally introduced by Williams and Martinez (2000) and accounts for allometric degree distributions and recent data on scaling relationships for species body mass and trophic levels (Riede et al., 2011). Each species i is fully characterised by its average adult body mass m_i. We sampled $\log_{10}$ body masses of animal species randomly with a uniform probability density from the inclusive interval $(2, 12)$ and the $\log_{10}$ body masses of plant species from the inclusive interval $(0, 6)$ (for empirical examples see Brose et al., 2019). This step makes the model inherently stochastic, but from hereon, all other steps are completely deterministic. The model is designed such that animal consumers feed on resources, which can be both plants and other animal species that are smaller than themselves. Body masses further determine the interaction strengths of feeding links as well as the metabolic demands of species.

Data from empirical feeding interactions are used to parametrise the functions that characterise the optimal prey body mass and the location and width of the feeding niche of a predator. From each m_i a unimodal attack kernel, called feeding efficiency, L_{ij}, is constructed which determines the probability of consumer species i to attack and capture an encountered resource species j. We model L_{ij} as an asymmetrical hump-shaped Ricker's function (equation T1-4) that is maximised for an energetically optimal resource body mass (optimal consumer-resource body mass ratio $R_{opt} = 100$) and has a width of $\gamma = 2$. The maximum of the feeding efficiency L_{ij} equals 1. Table B.S1 lists the full set of equations and table B.S2 is an overview of the standard parameter set for the equations. See also Schneider et al. (2016) for further information regarding the allometric food web model.

Table B.S1: Ordinary differential equations describing the local population dynamics driven by feeding interactions (see Schneider et al., 2016). We use the same allometric constraints and parameter ranges.

Equation No.	Model equations	Description
Equation T1-1	Animal population dynamics $\frac{dA_{i,z}}{dt} = e_P A_{i,z} \sum_j F_{ij,z} + e_A A_{i,z} \sum_k F_{ik,z} - \sum_k A_{k,z} F_{ki,z} - x_i A_{i,z}$	Rate of change of biomass density of animal species i on patch z; with conversion efficiency $e_P = 0.545$ typical for herbivory (Lang et al., 2017); conversion efficiency $e_A = 0.906$ typical for carnivory (Lang et al., 2017); feeding rate $F_{ij,z}$ of consumer i on resource j on patch z; metabolic demands per unit biomass for animals $x_i = x_A m_i^{-0.305}$ with scaling constant $x_A = 0.314$ (Ehnes et al., 2011; Yodzis and Innes, 1992). The first sum goes over all plant resources j, the second over all animal resources k and the third over all animal predators k of animal species i.
Equation T1-2	Functional response $F_{ij,z} = \frac{\omega_i \kappa_{i,j} R_{j,z}^{1+q}}{1 + c A_{i,z} + \omega_i \sum_k \kappa_{ik} h_{ik} R_{k,z}^{1+q}} \cdot \frac{1}{m_i}$	Per unit biomass feeding rate of consumer i as function of its own biomass density, A_i, (taking interference competition c, which is the time lost due to intraspecific encounters, sampled from a normal distribution with mean $\mu_c = 0.8$ and s.d. $\sigma_c = 0.2$ for each food web), and biomass density of the resource R_j (either animal A_j or plant species P_j); with ϕ_{ij}, resource specific capture coefficient (Eq. T1-3); h_{ij}, resource-specific handling time (Eq. T1-5); $\omega_i = 1/$(number of resource species of i), relative consumption rate accounting for the fact that a consumer has to split its consumption if it has more than one resource species.
Equation T1-3	Capture coefficient $\kappa_{ij} = \lambda_l m_i^{\beta_i} m_j^{\beta_j} L_{ij}$	Resource specific capture coefficient of consumer species i on resource species j scaling the feeding kernel L_{ij} by a power function of consumer and resource body mass, assuming that the encounter rate between consumer and resource scales with their respective movement speed. We sample the exponents β_i and β_j from normal distributions (mean $\mu_{\beta_i} = 0.42$, s.d. $\sigma_{\beta_i} = 0.05$; $\mu_{\beta_j} = 0.19$, s.d. $\sigma_{\beta_j} = 0.04$, respectively (Hirt et al., 2017b)). We divide here the group of consumer species into the subgroup of carnivorous and herbivorous species each comprising a constant scaling factor for their capture coefficients λ_l with $l \in 0, 1$ ($\lambda_0 = 40$ for carnivorous species and $\lambda_1 = 5000$ for herbivorous species); For plant resources, $m_j^{\beta_j}$ was replaced with the constant value of 1 (as plants do not move).
Equation T1-4	Feeding efficiency $L_{ij} = \left(\frac{m_i}{m_j R_{opt}} e^{1 - \frac{m_i}{m_j R_{opt}}} \right)^\gamma$	The probability of consumer i to attack and capture an encountered resource j (which can be either plant or animal), described by an asymmetrical hump-shaped curve (Ricker's function), with width $\gamma = 2$ centered around an optimal consumer-resource body mass ratio $R_{opt} = 100$.

Continued on next page

Table B.S1 – continued from previous page

Equation No.	Model equations	Description
Equation T1-5	Handling time $h_{ij} = h_0 m_i^{\eta_i} m_j^{\eta_j}$	The time consumer i needs to kill, ingest and digest resource species j, with scaling constant $h_0 = 0.4$ and allometric exponents η_i and η_j drawn from normal distributions with means $\mu_{\eta_i} = -0.48$ and $\mu_{\eta_j} = -0.66$, and standard deviations $\sigma_{\eta_i} = 0.03$ and $\sigma_{\eta_i} = 0.02$, respectively (Rall et al., 2012).
Equation T1-6	Plant population dynamics $\frac{dP_{i,z}}{dt} = r_i G_i P_{i,z} - \sum_k A_{k,z} F_{ki,z} - x_i P_{i,z}$	Rate of change of biomass density of plant species i on patch z; with predation loss $F_{ki,z}$ summed over all consumer species k feeding on plant species i; metabolic demands per unit biomass for plants $x_i = x_P m_i^{-0.25}$ with $x_P = 0.138$; intrinsic growth rate $r_i = m_i^{-0.25}$; species specific growth factor G_i (Eq. T1-7).
Equation T1-7	Growth factor for plants $G_i = min\left(\frac{N_1}{K_{i,1} + N_1}, \frac{N_2}{K_{i,2} + N_2}\right)$	Species-specific growth factor of plants determined dynamically by the most limiting nutrient $l \in 1, 2$; with $K_{i,l}$, half-saturation densities determining the nutrient uptake efficiency assigned randomly for each plant species i and nutrient l (uniform distribution within (0.1, 0.2)). The term in the minimum operator approaches 1 for high nutrient concentrations.
Equation T1-8	Nutrient dynamics $\frac{dN_{l,z}}{dt} = D(S_l - N_l) - \nu_l \sum_{i,z} r_i G_i P_{i,z}$	Rate of change of nutrient concentration N_l of nutrient $l \in \{1, 2\}$ on patch z, with global turnover rate $D = 0.25$, determining the rate at which nutrients are refreshed; supply concentration S_l, determining the maximum nutrient level of each nutrient, l, drawn from normal distributions with mean $\mu_S = 50$ and standard deviation $\sigma_S = 2$ (provided $S_l > 0$); relative nutrient content in plant species biomass ν_l ($\nu_1 = 1$, $\nu_2 = 0.5$).

B.S2 Generating landscapes

We generated differently fragmented landscapes, represented by random geometric graphs (Penrose, 2003), by randomly drawing the locations of Z patches from a uniform distribution between 0 and 1 for x- and y-coordinates respectively. We created landscapes of different size by scaling the maximum dispersal distance of all organisms δ_{max} with a factor, Q, to represent landscape sizes with edge lengths between 0.01 and 10. We obtained the number of patches, Z, by using a stratified random sampling approach, i.e. we added a random number drawn from an integer uniform distribution between 0 and 9 to a series of numbers of $10, 20, \ldots, 60$. Similarly, we set the landscape size, Q, by adding a random number drawn from a uniform distribution between 0 and 1 (respectively 0 and 0.1 for landscape sizes below 1) to a series of numbers of $0.01, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9, 1, 3, 5, 7, 9$.

B.S3 Dispersal

We model dispersal between local communities as a dynamic process of emigration and immigration, assuming dispersal to occur at the same timescale as the local population dynamics (Amarasekare, 2008). Thus, biomass flows dynamically between local populations and the dispersal dynamics directly influence local population dynamics and vice versa (Fronhofer et al., 2018). Similar approaches have been used by e.g. Abrams and Ruokolainen (2011) and Ims and Andreassen (2005). We model a hostile matrix between habitat patches that does not allow for feeding interactions to occur during dispersal, and thus, assume the biomass lost to the matrix to scale linearly with the distance travelled.

Emigration The total rate of emigration of species i from patch z is

$$E_{i,z} = d_{i,z} B_{i,z} \,, \tag{B.2}$$

with $d_{i,z}$ as the corresponding per capita dispersal rate. We model $d_{i,z}$ as

$$d_{i,z} = \frac{a}{1 + e^{b(x_i - v_{i,z})}} \,, \tag{B.3}$$

with a, the maximum dispersal rate, b, a parameter determining the shape of the dispersal rate (figure B.S1), x_i, the inflection point determined by the metabolic demands per unit biomass of species i, and $v_{i,z}$, the per capita net growth rate of species i on patch z. We chose to model $d_{i,z}$ as a function of each species' per capita net growth rate to account for emigration triggers such as resource availability, predation pressure and inter- and intraspecific competition (Bowler and Benton, 2005; Fronhofer et al., 2018). If for example an animal species' net growth is positive, there is no need for dispersal and emigration will be low. However, if the local environmental conditions deteriorate, the growing incentives to search for a better habitat increase the fraction of individuals emigrating. For plants, we assumed an additional scenario as there are examples of different life history strategies. There are for example plant species which disperse from their local habitat when they are doing well, i.e. they have a high net growth rate, as they can allocate more resources into reproduction resulting in higher seed dispersal (Miyazaki et al., 2009). However, there are also examples where plants reallocate resources into reproduction when they are doing poorly (Macedo, 2012) (figure B.S1b).

For each simulation run, a was sampled from a Gaussian distribution (μ_{aS}, σ_{aS}) and b was sampled from an integer uniform distribution within inclusive limits that differed between consumer and plant species (see table B.S2). The different intervals reflect different dispersal triggers for animals and plants.

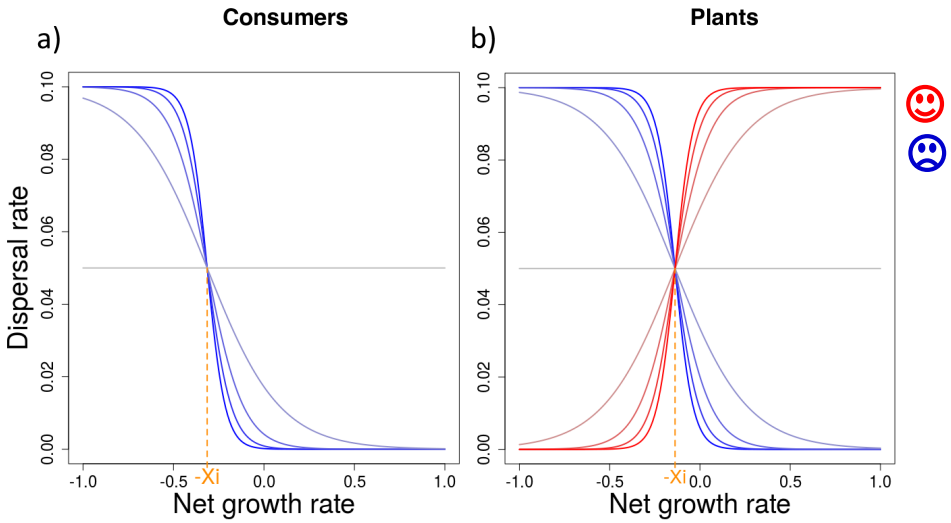

Figure B.S1: Functions illustrating the dispersal rate d_i for animal (a) and plant species (b), where x_i marks the inflection point for each species i determined by the metabolic demands (x_i) per unit biomass of species i (see table B.S1). The colours blue and red represent different dispersal strategies and the respective colour gradients depict the parameter range of b, which determines the slope of the dispersal rate (see equation B.3). For the purpose of illustration, we set the maximum dispersal rate to $a = 0.1$ and for animals and plants $x_{i_A} = 0.314$ and $x_{i_P} = 0.1384$, respectively.

Immigration The rate of immigration of biomass density of species i into patch z follows

$$I_{i,z} = \sum_{n \in N_z} E_{i,n}(1 - \delta_{i,nz}) \frac{1 - \delta_{i,nz}}{\sum_{m \in N_n} 1 - \delta_{i,nm}}, \tag{B.4}$$

where N_z and N_n are the sets of all patches within the dispersal range of species i on patches z and n, respectively. In this equation, $E_{i,n}$ is the emigration rate of species i from patch n, $(1 - \delta_{i,nz})$ is the fraction of successfully dispersing biomass, i.e. the fraction of biomass not lost to the matrix, and $\delta_{i,nz}$ is the distance between patches n and z relative to species i's maximum dispersal distance δ_i (see below paragraph Maximum dispersal distance). The term $\frac{1-\delta_{i,nz}}{\sum 1-\delta_{i,nm}}$ determines the fraction of biomass of species i emigrating from source patch n towards target patch z. This fraction depends on the relative distance between the patches, $\delta_{i,nz}$, and the relative distances to all other potential target patches m of species i on the source patch n, $\delta_{i,nm}$. Thus, the flow of biomass is greatest between patches with small distances. For numerical reasons, we did not allow for dispersal flows with $I_{i,z} < 10^{-10}$. In this case, we immediately set $I_{i,z}$ to 0.

Maximum dispersal distance Based on empirical observations (e.g. Jenkins et al., 2007) and previous theoretical frameworks (e.g. Holt, 2002; Jetz et al., 2004; Holt and Hoopes, 2005; Hirt et al., 2017a), we assume that the maximum dispersal distance δ_i of animal species increases with their body mass. For animal species, the body mass m_i determines how fast and how far they can travel through the matrix

Table B.S2: Model parameters and output variables.

Parameter	Description	Value
	Trophic interactions between species	
e_A	conversion efficiency animal species	0.906; (Lang et al., 2017)
e_P	conversion efficiency plant species	0.545; (Lang et al., 2017)
x_A	scaling constant metabolic demands animal species	0.314; (Yodzis and Innes, 1992)
x_P	scaling constant metabolic demands plant species	0.138; (Yodzis and Innes, 1992)
μ_c, σ_c	mean and standard deviation for interference competition	0.8, 0.2
λ_0	scaling factor capture coefficient for carnivorous species	40
λ_1	scaling factor capture coefficient for herbivorous species	5000
μ_{β_i}, σ_{β_i}	mean and standard deviation allometric exponent for attack rates consumer	0.42, 0.05; (Hirt et al., 2017b)
μ_{β_j}, σ_{β_j}	mean and standard deviation allometric exponent for encounter of prey	0.19, 0.04; (Hirt et al., 2017b)
ω_i	relative consumption rate	$\frac{1}{\text{number of prey species } i}$
R_{opt}	optimal consumer-resource body mass ratio	100
γ	scaling exponent Ricker's function	2
h_0	scaling factor handling time	0.4
μ_{η_i}, σ_{η_i}	mean and standard deviation allometric exponent handling time consumer	-0.48, 0.03; (Rall et al., 2012)
μ_{η_j}, σ_{η_j}	mean and standard deviation allometric exponent handling time resource	-0.66, 0.02; (Rall et al., 2012)
μ_q, σ_q	mean and standard deviation hill coefficient	1.5, 0.2
	Nutrient dynamics	
K	half saturation density nutrient uptake	(0.1, 0.2)
D	nutrient turnover rate	0.25
μ_{S_l}, σ_{S_l}	mean and standard deviation of nutrient supply concentration	50, 2
ν_1, ν_2	relative nutrient content in plant species biomass	1, 0.5
	Dispersal dynamics	
δ_{max}	species-specific maximum dispersal distance	0.5
ϵ	scaling exponent for species-specific maximum dispersal distance	0.05
μ_{a_S}, σ_{a_S}	mean and standard deviation of max. emigration	0.1, 0.03
θ	cut off emigration function	$3 \cdot \sigma_{a_S}$
b	shape parameter of the emigration function	(0,19) (cons.) (-20,19) (plants)
	Output variables	
$\overline{\tau}$	mean distance between all habitat patches, with τ_{nm}, the absolute distance between patches n and m, and $(Z^2 - Z)$, the total number of potential directed links between all Z habitat patches	$\frac{\sum_{n,m=1}^{Z} \tau_{nm}}{Z^2 - Z}$
ρ_i	landscape connectance of species i, with L_i, the number of directed dispersal links of species i	$\frac{L_i}{Z^2 - Z}$

before needing to rest and feed in a habitat patch. Thus animal species at high trophic positions can disperse further than smaller animals at lower trophic levels. Each animal species perceives its own dispersal network dependent on its species-specific maximum dispersal distance

$$\delta_i = \delta_0 m_i^{\epsilon}\,, \tag{B.5}$$

where the exponent $\epsilon = 0.05$ determines the slope of the body mass scaling of δ_i. We chose a positive value for ϵ to account for a higher mobility of animals with larger body masses. The intercept $\delta_0 = 0.1256$ was chosen such that the animal species with the largest possible body mass of $m_i = 10^{12}$ had a maximum dispersal distance of $\delta_i = 0.5$. Thus, the animal species with the smallest possible body mass of $m_i = 10^2$ had a maximum dispersal distance of $\delta_i = 0.158$.

As plants are passive dispersers driven by e.g. wind with no clear relationship between body mass and dispersal distance, we model their maximum dispersal distance as random and body mass independent (Jenkins et al., 2007). We sampled δ_i for each plant species from a uniform probability density within the interval $(0, 0.5)$. Thus, the best plant disperser can potentially have the same maximum dispersal distance as the largest possible animal species (table B.S2). Additionally, we tested a null model in which all species have the same maximum dispersal distance of $\delta_i = \delta_{max}$. See section B.S8 for further information on the additional simulations.

B.S4 Numerical simulations and data analysis

We constructed 30 model food webs, each comprising 10 plant and 30 animal species. To avoid confounding effects of different initial species diversities, we kept both the number of species S and the fraction of plants and animals constant among all food webs. For each simulation, we randomly generated a landscape of size Q (edge length of a square landscape) with Z randomly distributed habitat patches. To test each food web across a gradient of number of habitat patches and habitat isolation, we drew the number of habitat patches, Z, from the inclusive interval $(10, 69)$ and the size of the landscape, Q, from the inclusive interval $(0.01, 10)$ using a stratified random sampling approach (see also section B.S2 for further information). With this approach, we generated landscapes on two independent gradients covering two aspects of fragmentation, namely number of fragments and habitat isolation. To cover the full parameter range of Z and Q, we simulated each food web on 72 landscapes resulting in a total of 2160 simulations. We achieved a full range for the gradient of habitat isolation (landscape connectance ranging from 0 to 1, figure B.S3c). The upper limit for the number of patches was chosen to conform to the maximum usage time of 10 days per simulation on the high-performance-cluster we used (*EVE - High-Performance Computing Cluster*). Additionally, we performed dedicated simulation runs to reference the two extreme cases, i.e. (1) landscapes in which all patches are direct neighbours without a hostile matrix, and thus, no dispersal mortality, and (2) fully isolated landscapes, in which no species can bridge between patches, and thus, a dispersal mortality of 100% .

For each simulation run, we initialised our model with random conditions: Each habitat patch z holds a random selection of 21 to 40 species (with each of the 40 species of the full food web existing on at least one patch) and initial biomass densities $B_{i,z}$ and nutrient concentrations N_l ($l \in 1, 2$) were randomly sampled with uniform probability density within the intervals $(0, 10)$ for $B_{i,z}$ and $(S_l/2, S_l)$ for N_l, respectively. Here, S_l are the supply concentrations of the nutrients, which are constant on all habitat patches but differ between the two nutrients. See table B.S2, Equation T1-8 and Schneider et al. (2016) for further information on the nutrient dynamics.

Starting from these random initial conditions, we numerically simulated local food web and dispersal dynamics over 50,000 time steps by integrating the system of differential equations implemented in C++ using procedures of the SUNDIALS CVODE solver version 2.7.0 (backward differentiation formula with absolute and relative error tolerances of 10^{-10} (Hindmarsh et al., 2005)). Successful dispersal between local populations thereby enabled species to establish populations on patches where they were initially absent. For numerical reasons, a local population was considered extinct once $B_{i,z} < 10^{-20}$, and $B_{i,z}$ was then immediately set to 0.

B.S4.1 Output variables

We recorded the following output variables for each simulation run: (1) the mean biomass density of each species i on each habitat patch z over the last 20,000 time steps, $\overline{B}_{i,z}$; (2) the number of habitat patches in a landscape, Z; (3) habitat isolation, i.e. the mean distance between all habitat patches, $\overline{\tau}$ (see table B.S2); and (4) the landscape connectance of each species i, ρ_i (see table B.S2). Thus, ρ_i determines the ability of a species to connect habitat patches in a fragmented landscape.

Statistical models and data visualisation We tested for correlation between initialised and emerged β-diversity, which was however not the case (see section B.S9). Further, we used generalised additive mixed models (GAMM) from the mgcv package in R (Wood, 2017) to visualise the impact of number of patches and habitat isolation on species diversity. To fit the model assumptions, we logit-transformed $\overline{\alpha}$-diversity, and log-transformed β-diversity. We analysed each diversity index separately, with the number of patches Z (log-transformed), the mean patch distance $\overline{\tau}$ (log-transformed) and their interaction as fixed effects and the ID of the food web (1 - 30) as random factor (with normal distribution for $\overline{\alpha}$- and β-diversity, and binomial distribution for γ-diversity). Similarly, we analysed the mean biomass densities, $\overline{B}_{i,z}$ (log-transformed), and species-specific landscape connectance, ρ_i, for each species (ID 1 - 40) using GAMM with a normal distribution.

B.S4.2 Analysis

Out of the 2160 simulations we started, 57 were terminated by reaching the maximum usage time of 10 days per simulation on the high-performance-cluster we used (*EVE - High-Performance Computing Cluster*). We further deleted 30 simulations as they had entirely isolated landscapes with no dispersal links. We performed all statistical analyses in R version 3.3.2. (R Core Team, 2016) using the output of the remaining 2073 simulations. See also section B.S8 for additional information.

Species diversity We quantified Whittaker's α-, β-, and γ-diversity (Whittaker, 1972) using presence-absence data derived from the recorded mean biomass densities, $\overline{B}_{i,z}$, counting species i present on patch z when $\overline{B}_{i,z} > 10^{-20}$. In Whittaker's approach, α accounts for the local species richness, β is the component of regional diversity that accumulates from compositional differences between local communities, and γ is the regional diversity, i.e. the species richness at the landscape scale (Whittaker, 1972). We relate α, β and γ to each other using multiplicative partitioning (Whittaker, 1972), i.e. $\alpha \cdot \beta = \gamma$. Here, we use α averaged over all habitat patches Z (which we hereafter refer to as $\overline{\alpha}$) to get a measure at the landscape level comparable to β and γ.

B.S5 Maximum trophic level

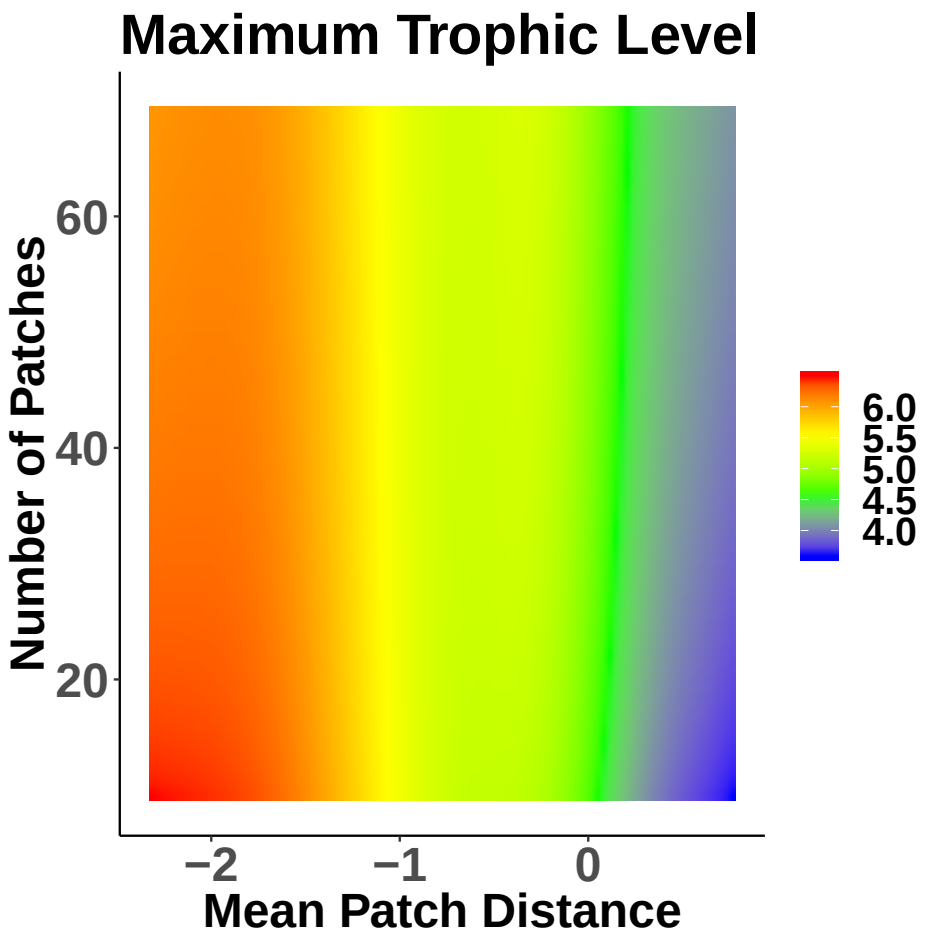

Figure B.S2: Heatmap visualising the maximum trophic level within a food web (colour-coded; z-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis) and the number of habitat patches (Z; y-axis). The heatmap was generated based on the statistical model predictions. The loss of species diversity driven by habitat isolation also translates into a loss of the maximum trophic level.

B.S6 Additional simulations with a constant maximum dispersal distance

We repeated all simulations with a constant maximum dispersal range for all species of $\delta_{const.} = 0.5$, i.e. all species have the same spatial network, to understand the effect of the dispersal advantage of larger animals. The results from these simulations are very similar to the results with the species-specific scaling of dispersal ranges, showing the same biomass density drop of larger animals at low mean distances (figure B.S3).

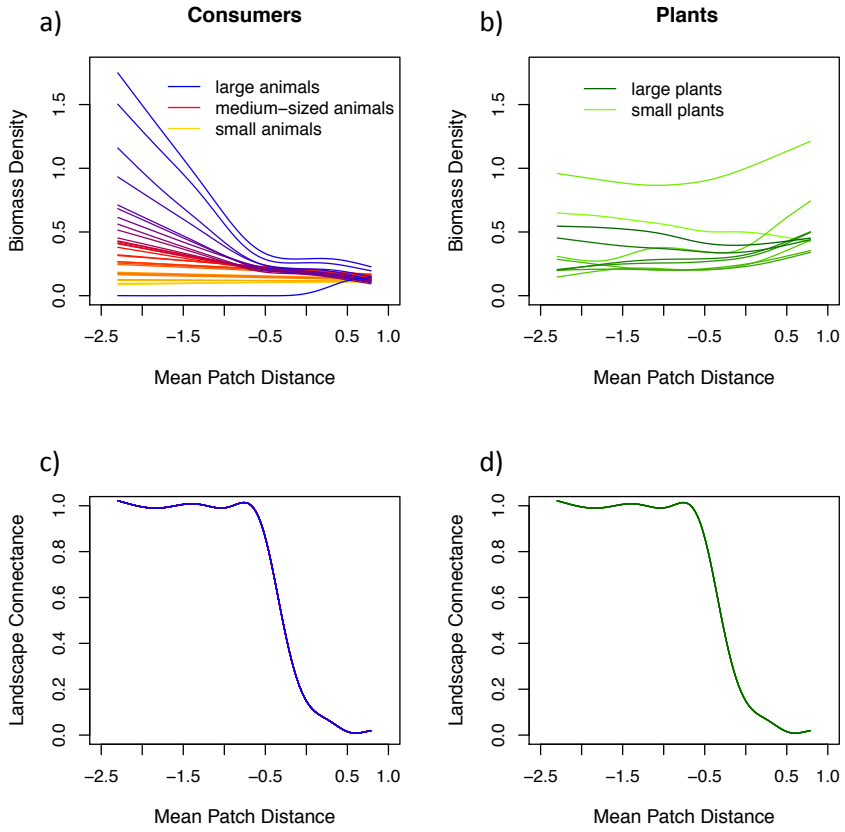

Figure B.S3: Top row: Mean biomass densities of consumer (a) and plant species (b) over all food webs (B_i, $\log_{10}$-transformed; y-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Each colour depicts the biomass density of species i averaged over all food webs: (a) colour gradient where orange represents the smallest, red the intermediate and blue the largest consumer species; (b) colour gradient where light green represents the smallest and dark green the largest plant species. Bottom row: Mean species-specific landscape connectance (ρ_i; y-axis) for consumer species (c) and plant species (d) over all food webs as a function of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis), using the same maximum dispersal distance for all species, $\delta_{const} = 0.5$.

B.S7 Additional simulations of the two extreme cases

To explore the extreme cases of fragmentation in our model framework, we conducted additional simulations with emigration but no immigration on patches to represent completely isolated patches (disconnected), and landscapes with patches containing all species of the meta-food-web and neither emigration nor immigration to represent one joint landscape with no fragmentation (joint). For the disconnected scenario we simulated 12 replicates for each of the 30 food webs covering in the same stratified random gradient of patch numbers between 10 and 69 as in the main simulations and were also initialised with a subset of species (see section B.S4). For the joint scenario we simulated 20 replicates for each food web containing 2 independent patches initialised with all species and no dispersal.

(1) Joint scenario with no dispersal mortality $\overline{\alpha}$-diversity is on average 37.621, γ-diversity 37.172 and β-diversity 1.004 (figure B.S4, purple triangle).

(2) Fully isolated scenario with 100% dispersal mortality $\overline{\alpha}$-diversity is on average 11.945, γ-diversity 32.801 and β-diversity 2.876 (figure B.S4, orange triangle).

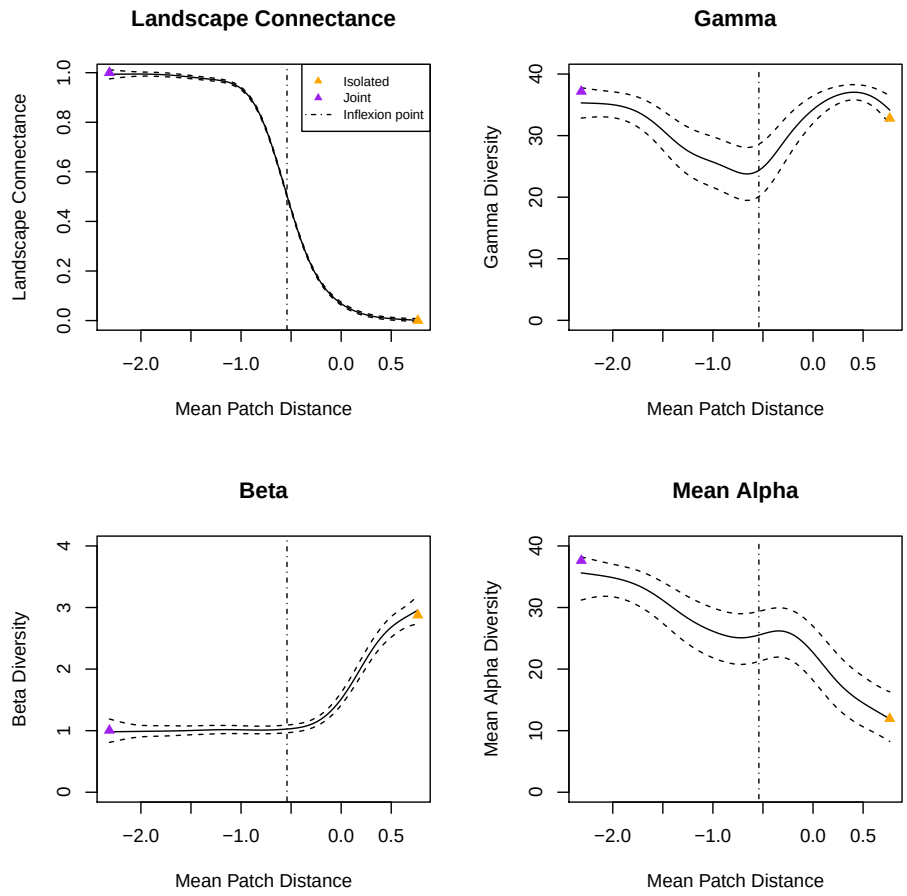

Figure B.S4: Shown are model predictions for landscapes with 40 patches across the whole gradient of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Top-left panel shows the landscape connectance averaged over all species (y-axis) as response to the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Subsequent panels show γ-diversity, β-diversity and $\overline{\alpha}$-diversity (y-axes) in response to the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Purple triangles represent reference points from dedicated simulations in a joint scenario and orange triangles for fully isolated scenarios (see section B.S7.

B.S8 Sensitivity analysis

We tested the effect of randomly drawn dispersal parameters (maximum dispersal rate, a, and the shape of the dispersal function, b; equation B.3) on $\overline{\alpha}$-, β- and γ-diversity for consumers and plants respectively. We used generalised additive mixed models (GAMM) from the mgcv package in R for all sensitivity analyses. To fit the model assumptions, we logit-transformed $\overline{\alpha}$-diversity, and log-transformed β- and γ-diversity.The emigration parameters were separately used as fixed effects and the ID of the food web (1 - 30) as random factor (with normal distribution for $\overline{\alpha}$- and β-diversity, and binomial distribution for γ-diversity). Both parameters show no strong effect in all tested cases (figure B.S5 - B.S7). Only the maximum emigration rate a of consumers shows a small negative effect on $\overline{\alpha}$-diversity (figure B.S5). As a higher maximum emigration rate results in an overall larger loss term due to dispersal, this fits to our general findings.

Additional sensitivity analysis for interference competition, allometric exponent for attack rates of consumer species, exponents for handling time, hill coefficient and nutrient turnover rate were omitted as they were tested thoroughly in Schneider et al. (2016). There, the dynamics of the food web model were shown to be robust to changes in model parameters. For each of the 2073 simulation runs the parameters of the trophic interactions were independently sampled from appropriate probability distributions within ecologically reasonable limits (see table B.S1). To account for the stochastic nature of the algorithm provided by Schneider et al. (2016) by which food web topologies are created, we generated an ensemble of 30 food webs by randomly sampling 30 sets of species body masses.

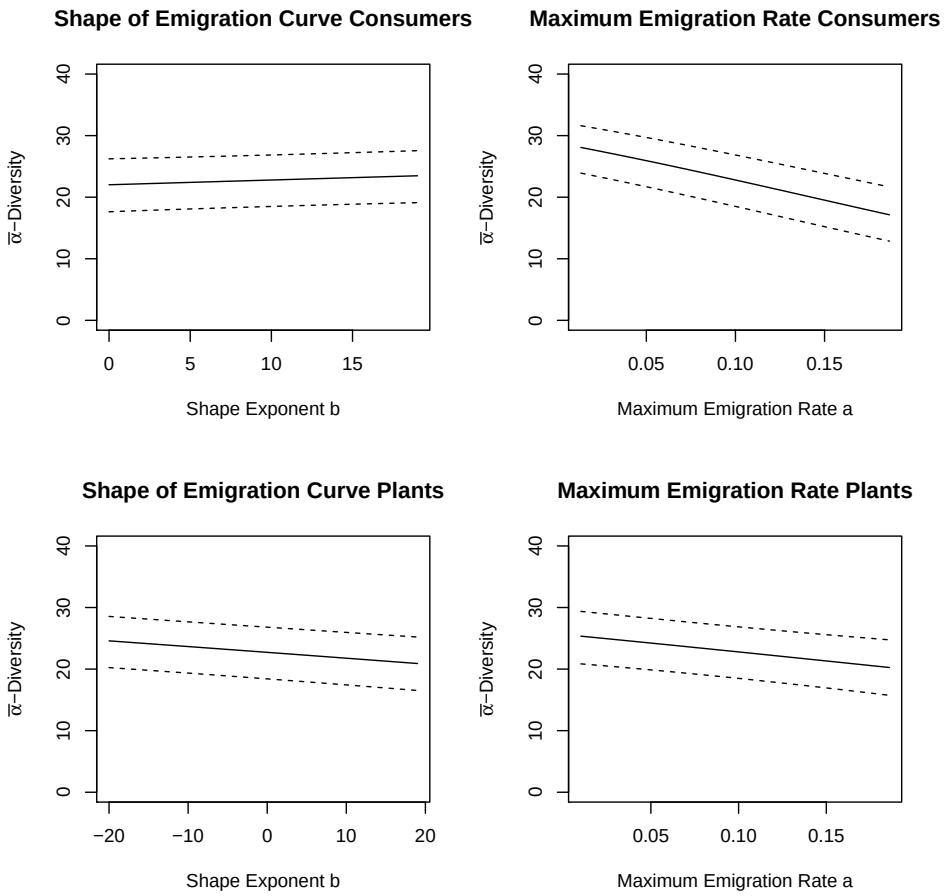

Figure B.S5: $\overline{\alpha}$-diversity (y-axes) of consumers and plants in dependence of the maximum emigration rate, a, and the shape of the emigration function, b respectively (x-axes).

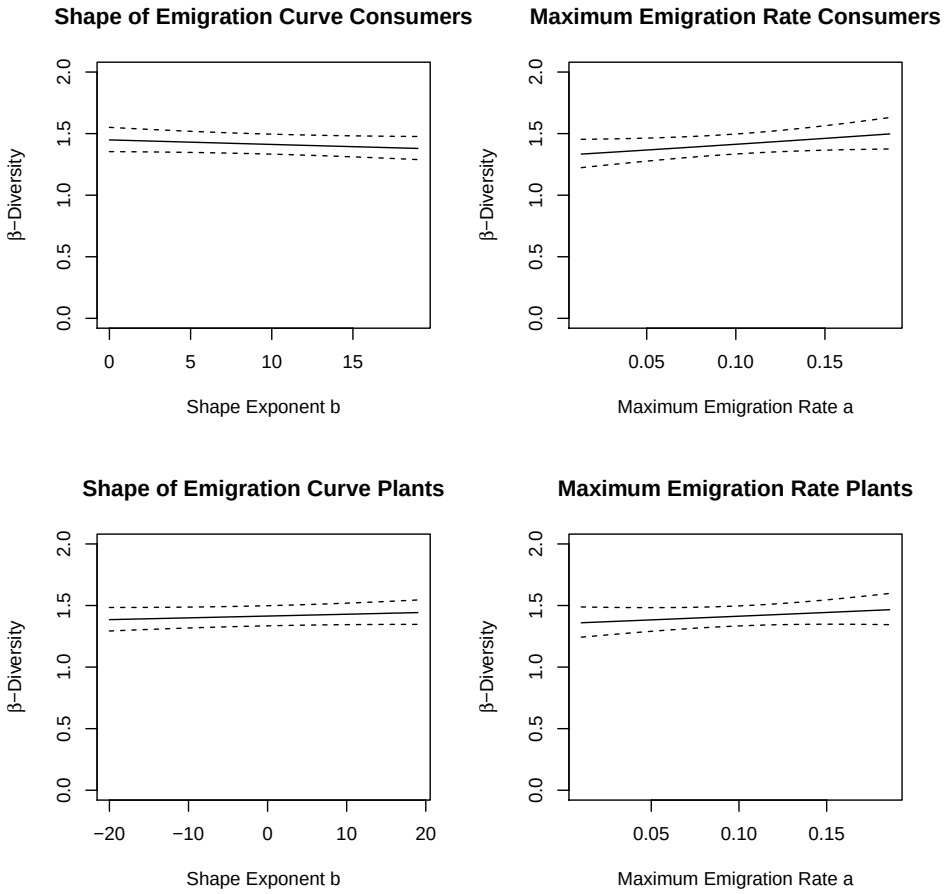

Figure B.S6: β-diversity (y-axes) of consumers and plants in dependence of the maximum emigration rate, a, and the shape of the emigration function, b respectively (x-axes).

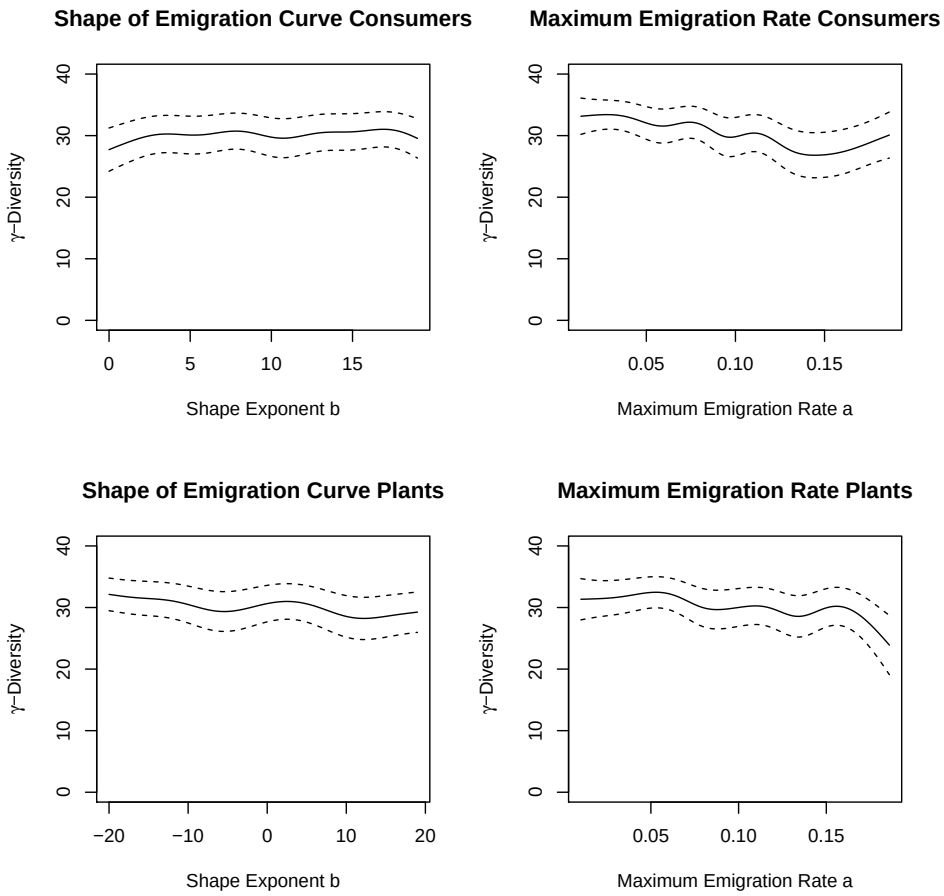

Figure B.S7: $\gamma-$diversity (y-axes) of consumers and plants in dependence of the maximum emigration rate, a, and the shape of the emigration function, b respectively (x-axes).

B.S9 Initial and post-simulation β-diversity

To see how the initialised β-diversity (see section B.S4) influenced the post-simulation β-diversity we performed a generalised additive mixed model (GAMM) from the mgcv package in R with the initial β-diversity as fixed effect and the post-simulation β-diversity as the response variable. Both were log-transformed to fit model assumptions. The post-simulation β-diversity and initial β-diversity were not correlated. This suggests that the initial β-diversity which is due to initialising the patches in the landscape with only a subset of species from the regional species pool does not influence the post-simulation β-diversity detectably (approximate p-value: 0.518) (figure B.S8).

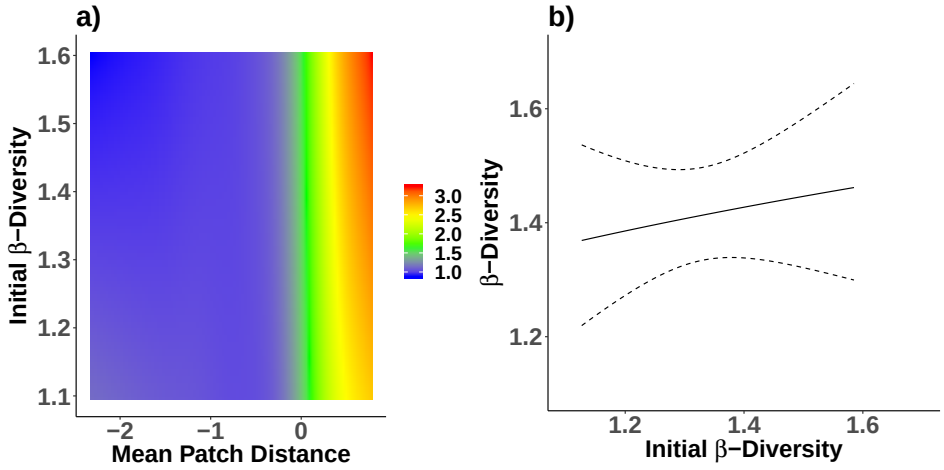

Figure B.S8: (a) Heatmap visualising β-diversity (colour-coded; z-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis) and the initial β-diversity (y-axis). The heatmap was generated based on the statistical model predictions. (b) The post-simulation β-diversity (y-axis) and the initial β-diversity (x-axis) were not correlated. In strongly isolated landscapes β-diversity increases slightly with higher initial β-diversity. However, post-simulation β-diversity is higher than the initial β-diversity.

B.S10 Standard errors in biomass densities

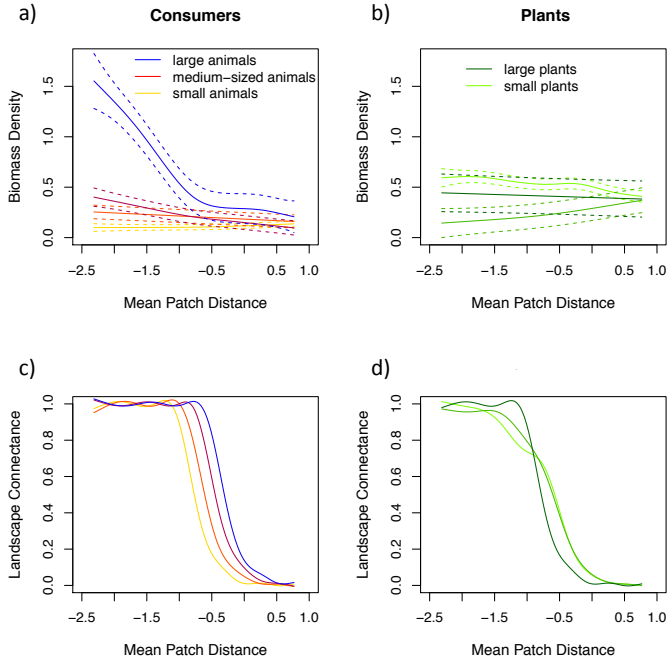

Figure B.S9: Top row: Mean biomass densities [$\log_{10}$(biomass density +1)] with standard errors [± 2*SE] for four exemplary animal consumer species (a) and three exemplary basal plant species (b) over all food webs (B_i, $\log_{10}$-transformed; y-axis) in response to habitat isolation, i.e. the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis). Each colour depicts the biomass density of species i averaged over all food webs: (a) colour gradient where orange represents the smallest, red the intermediate and blue the largest consumer species; (b) colour gradient where light green represents the smallest and dark green the largest plant species. Bottom row: Mean species-specific landscape connectance (ρ_i; y-axis) for consumer (c) and plant species (d) over all food webs as a function of the mean patch distance ($\overline{\tau}$, $\log_{10}$-transformed; x-axis).

C

Supplementary Information for Research Chapter 2

Johanna Häussler, György Barabás & Anna Eklöf. 2020 ”A Bayesian network approach to trophic metacommunities shows habitat loss accelerates top species extinctions”. Ecology Letters 23: 1849–1861.

A Bayesian network approach to trophic metacommunities shows habitat loss accelerates top species extinctions

Supporting Information

Johanna Häussler, György Barabás & Anna Eklöf

S1 Bayesian Networks

A Bayesian network is a graphical model for the probabilistic relationships among a set of variables (Jensen 1996, Eklöf *et al.* 2013). In the context of food webs, the probability of each species going extinct is a function of the probabilities of its resources going extinct.

More specifically, a species C has, first of all, a baseline probability of extinction π_C; the species goes extinct with this likelihood even if it has full access to its resources. Such a baseline extinction probability may be related, for instance, to the fact that individual habitat patches are small in size, supporting only a few individuals and therefore prone to extinction via demographic stochasticity. Second, if the species has access to only a subset of its resources, its extinction probability increases, reaching 1 when all resources are absent.

Let species C have two prey items, A and B (the results below are straightforwardly generalizable to an arbitrary number of prey), and assume that the conditional probabilities of species C being absent given the presence or absence of its prey items are known: $P(\neg C|AB)$ is the probability that C is extinct given that both its prey are present; $P(\neg C|\neg AB)$ is the probability that C is extinct given that prey A is absent but prey B is present; and so on. To obtain the marginal probability $P(\neg C)$ of C going extinct, we use the law of total probability:

$$\begin{aligned} P(\neg C) = {} & P(\neg C|AB)P(A)P(B) + P(\neg C|\neg AB)P(\neg A)P(B) \\ & + P(\neg C|A\neg B)P(A)P(\neg B) + P(\neg C|\neg A\neg B)P(\neg A)P(\neg B) \ . \end{aligned} \tag{S1}$$

In principle, the conditional probabilities may be as complicated as demanded by the natural history of the modeled ecological scenario. For instance, it is possible to have $P(\neg C|AB) > P(\neg C|\neg AB)$, with the probability of extinction greater in the presence of two alternative prey items than with only one. For example, if species A and B are mutualists (for example, A emits an alarm call when a predator is present, alerting members of both A and B), then the absence of A may in fact make predation easier for C.

Here, however, we operate with the simple assumption that the conditional probabilities of species C going extinct depend only on the fraction f of its resources lost. (We relax this assumption later, in Section S7.) We model this conditional probability as

$$P(\neg C|f) = \pi_C + (1-\pi_C)w(f) \ , \tag{S2}$$

where the weighting function $w(f)$ is monotonically increasing and defined for $0 \leq f \leq 1$, such that $w(0) = 0$ and $w(1) = 1$. The former condition holds when all resources are present, in which case Eq. S2 yields $P(\neg C|0) = \pi_C$, the baseline extinction probability. The latter condition means that when all resources are lost, $P(\neg C|1) = 1$: no species can survive without any resources sustaining it.

To see how this is applied, let us assume both A and B are basal species. We then have $P(\neg A) = 1 - P(A) = \pi_A$, and the same for species B. Using Eq. S2 in Eq. S1:

$$\begin{aligned} P(\neg C) = {} & [\pi_C + (1-\pi_C)w(0)](1-\pi_A)(1-\pi_B) + [\pi_C + (1-\pi_C)w(1/2)]\pi_A(1-\pi_B) \\ & + [\pi_C + (1-\pi_C)w(1/2)](1-\pi_A)\pi_B + [\pi_C + (1-\pi_C)w(1)]\pi_A\pi_B \ . \end{aligned} \tag{S3}$$

To make further progress, one must specify the form of $w(f)$. For instance, if $w(f) = f$, then

$$P(\neg C) = \pi_C(1-\pi_A)(1-\pi_B) + \left(\frac{1+\pi_C}{2}\right)\pi_A(1-\pi_B) + \left(\frac{1+\pi_C}{2}\right)(1-\pi_A)\pi_B + \pi_A\pi_B \ . \tag{S4}$$

For example, if $\pi_A = \pi_B = \pi_C = 0.1$, then Eq. S4 gives $P(\neg C) = 0.19$ (and $P(C) = 1 - P(\neg C) = 0.81$). The marginal probability of extinction can be calculated analogously for any species with any number of resource items. However, when the resource species are not basal, one should use the (already calculated) marginal persistence and extinction probabilities of the prey in Eq. S1. Thus, determining the extinction probabilities of all species is a bottom-up calculation process: we start with basal species, then move on to species only consuming those basal species, and so on, to the very top of the food web.

This also means that the Bayesian network approach has two important limitations. First, the food webs must be acyclic, as otherwise this bottom-up approach would not work. Second, top-down effects cannot be implemented, since the loss of the top predator from the system has no effect on the persistence probabilities of species at lower trophic levels.

S2 The trophic metacommunity model

We generalize single-species metapopulation models on fragmented landscapes (Hanski & Ovaskainen 2000, Ovaskainen & Hanski 2001, Hanski & Ovaskainen 2003, Grilli *et al.* 2015) to trophic communities. Let S be the number of species, N the number of habitat patches, and p_i^k the probability that species i is found in patch k. The basic model reads

$$\frac{\mathrm{d}p_i^k}{\mathrm{d}t} = (1-p_i^k)C_i^k - p_i^k E_i^k \ , \tag{S5}$$

where C_i^k and E_i^k are the colonization and extinction rates of species i in patch k; both may depend on the patch occupancies p_i^k. Here and elsewhere we follow the convention that subscripts denote species indices and superscripts denote patch indices.

For our trophic metacommunity approach, we model colonization using a species-dependent landscape matrix:

$$C_i^k = \sum_{l=1}^{N} M_i^{kl} p_i^l \tag{S6}$$

(Ovaskainen & Hanski 2001), where M_i^{kl}, the (k,l)th entry of species i's landscape matrix, is the rate of dispersal of species i from patch l to k. In turn, the extinction rates are modeled based on the probability of extinction δ_i^k of species i in patch k per unit time. To convert this probability into the rate E_i^k, we treat extinction as a Poisson process. This is justified on the grounds that metapopulation approaches assume a time scale separation between migration and local population dynamics, with the former being much slower than the latter (Hanski 1994). This allows one to treat populations in local patches as being in population dynamical quasi-equilibrium. In this quasi-equilibrium state, there is some constant probability of going extinct per unit of time in each patch, leading to the Poisson process with rate parameter E_i^k:

$$\delta_i^k = 1 - \exp(-E_i^k) \ . \tag{S7}$$

This yields an extinction probability of 0 when E_i^k is zero, and a probability of one for E_i^k infinitely large. Solving for the rate, we get

$$E_i^k = -\log(1-\delta_i^k) \ . \tag{S8}$$

The essence of our approach to trophic metacommunities is the way we model the extinction probabilities δ_i^k. These are calculated from a Bayesian network representation of the food web. Given baseline extinction probabilities π_i^k for species i in patch k, we equate δ_i^k with the marginal probability of extinction in patch k, calculated from the Bayesian network. Since δ_i^k is the probability of extinction per unit time (during which no colonization events happen due to the time scale separation between local

dynamics and dispersal mentioned above), the probability of a species being present in a given patch k is the product of two probabilities: the local probability $P^k(i) = 1 - P^k(\neg i)$ of persistence from the Bayesian network, multiplied by the probability that species i is present in patch k in the first place. This latter probability is by definition the patch occupancy p_i^k, and so, when applying Eq. S1 to obtain the extinction probability of a species i, we perform the

$$1 - P^k(\neg\text{prey}) \rightarrow (1 - P^k(\neg\text{prey}))p_{\text{prey}}^k \tag{S9}$$

replacement (see Section S4 for example applications).

For basal species, we assume that the nutrients they use are always available. This leads to $p_j^k = 1$ in all patches for all nutrients j, so for basals, $\delta_{\text{basal}}^k = 1 - (1 - \pi_{\text{basal}}^k)p_j^k = \pi_{\text{basal}}^k$.

S3 Simple model properties

For a single focal species, Eq. S5 belongs in the class of spatially realistic Levins models in which there is a single measure of the metapopulation capacity, defined as the leading eigenvalue of $\partial g_i^k / \partial p_i^l$ evaluated at $p_i^k = 0$ (Ovaskainen & Hanski 2001), where $g_i^k = C_i^k / E_i^k$ is the model's principal map. Using Eqs. S6 and S8, the principal map reads

$$g_i^k = -\frac{1}{\log(1 - \delta_i^k)} \sum_{l=1}^{N} M_i^{kl} p_i^l \,. \tag{S10}$$

Due to our Bayesian network approach, the extinction likelihood δ_i^k is a function of the patch occupancies of the focal species' prey, but not those of the focal species itself. That is, δ_i^k is independent of p_i^k. The Jacobian of the principal map evaluated at $p_i^k = 0$, which we will denote by A_i^{kl}, therefore simply reads

$$A_i^{kl} = \left.\frac{\partial g_i^k}{\partial p_i^l}\right|_{p_i^k = 0} = -\frac{M_i^{kl}}{\log(1 - \delta_i^k)} \,. \tag{S11}$$

The metapopulation capacity λ_i of species i is the leading eigenvalue of this matrix. If λ_i exceeds 1, the metapopulation persists at equilibrium, otherwise all p_i^k are zero.

To obtain the equilibrium patch occupancies, we set $\mathrm{d}p_i^k/\mathrm{d}t = 0$ in Eq. S5. The equilibrial patch occupancy distribution is then expressed as $C_i^k/(C_i^k + E_i^k) = g_i^k/(g_i^k + 1)$. Defining the map

$$h_i^k = \frac{g_i^k}{g_i^k + 1} \,, \tag{S12}$$

the equilibrial p_i^k can be obtained by iterating this map until its fixed point is reached. In spatially realistic Levins-type models like Eq. S5, the equilibrium state is unique and stable with respect to this iteration scheme (Ovaskainen & Hanski 2001). This means that the iteration eventually converges to the true equilibrium values for any valid nonzero starting condition, yielding an efficient numerical method for finding the equilibrium patch occupancies.

The value of a given habitat patch k to a metapopulation i is defined as $V_i^k = (\lambda_i - \lambda_i^{-k})/\lambda_i$, where λ_i^{-k} denotes species i's metapopulation capacity after removing patch k. For models like Eq. S5, this relative decrease can be obtained as

$$V_i^k = \frac{v_i^k w_i^k}{\sum_{l=1}^{N} v_i^l w_i^l} \,, \tag{S13}$$

where v_i^k is the left and w_i^k the right eigenvector belonging to the leading eigenvalue giving the metapopulation capacity (Ovaskainen & Hanski 2001). Patches can be ranked using this formula, from most to least important for persistence (the most important causing the largest relative decline in the metapopulation capacity, and vice versa). This ranking is local in the sense that it is not preserved after removing a patch: after removal, the patch values must be recalculated using Eq. S13. In practice, removing a small fraction

of patches will only alter the rankings by a small amount, so this recalculation needs not to happen after the removal of every single patch.

The average patch occupancy at equilibrium, $\overline{p}_i$, can be approximated as

$$\overline{p}_i \approx 1 - \frac{1}{\lambda_i} , \tag{S14}$$

where λ_i is the metapopulation capacity for species i (the leading eigenvalue of A_i^{kl} in Eq. S11). Formally, this approximation works best for the weighted average

$$\overline{p}_i = \sum_{k=1}^{N} p_i^k V_i^k \tag{S15}$$

(Ovaskainen & Hanski 2001). However, Eq. S14 works acceptably even for the simple average $\overline{p}_i = \sum_{k=1}^{N} p_i^k / N$.

S4 Analytically tractable trophic networks

S4.1 One consumer, one resource

The simplest example of a trophic metacommunity consist of just two species: one consumer C and one basal resource R. Below we analyze the trophic metacommunity formed by these species, step by step.

Step 1: Solve for the extinction probabilities using the Bayesian network approach. The baseline probabilities of extinction for the resource and the consumer are π_R^k and π_C^k, respectively. Since R is a basal species, we have $P^k(\neg R) = \pi_R^k$. The resource's probability of extinction in a patch with resource occupancy p_R^k is written using Eq. S9: $\delta_R^k = 1 - (1 - P^k(\neg R))p_R^k = 1 - (1 - \pi_R^k)p_R^k$. We now obtain the consumer's marginal probability of extinction δ_C^k in the style of Eq. S1, except with only a single resource and applying Eq. S9:

$$\begin{aligned} \delta_C^k &= P^k(\neg C|R)P^k(R) + P^k(\neg C|\neg R)P^k(\neg R) \\ &= P^k(\neg C|R)(1-\pi_R^k)p_R^k + P^k(\neg C|\neg R)[1-(1-\pi_R^k)p_R^k] . \end{aligned} \tag{S16}$$

Using Eq. S2 to write the conditional probabilities, and noting that $w(0) = 0$ and $w(1) = 1$ regardless of the form of $w(f)$, we get $P^k(\neg C|R) = \pi_C^k$ and $P^k(\neg C|\neg R) = 1$:

$$\delta_C^k = \pi_C^k(1-\pi_R^k)p_R^k + 1 - (1-\pi_R^k)p_R^k . \tag{S17}$$

Rearranging, and writing out the marginal extinction probabilities of both species:

$$\delta_R^k = \pi_R^k , \tag{S18}$$

$$\delta_C^k = 1 - (1-\pi_C^k)(1-\pi_R^k)p_R^k . \tag{S19}$$

Step 2: Obtain the metapopulation capacity of each species. We first calculate the Jacobian matrix of each species' principal map evaluated at zero. Substituting Eqs. S18 and S19 into Eq. S11:

$$A_R^{kl} = -\frac{M_R^{kl}}{\log(1-\pi_R^k)} , \tag{S20}$$

$$A_C^{kl} = -\frac{M_C^{kl}}{\log[(1-\pi_C^k)(1-\pi_R^k)p_R^k]} . \tag{S21}$$

The metapopulation capacities are given by the leading eigenvalues λ_R and λ_C of A_R^{kl} and A_C^{kl}, respectively. For persistence, they must exceed 1. To evaluate λ_C, one must know p_R^k beforehand—this can be obtained e.g. by iterating Eq. S12 for the basal species.

Step 3: Approximate metapopulation capacities analytically. In general, to get a meaningful non-numerical answer for the metapopulation capacities, we must simplify the problem. This can be done in two steps:

Step 3a: Replace quantities with their averages. This is done by performing the $\pi_i^k \to \pi_i$, $p_i^k \to \overline{p}_i$ substitutions in the expressions for the A_i^{kl}. Eqs. S20 and S21 then read

$$A_R^{kl} \approx -\frac{M_R^{kl}}{\log(1-\pi_R)} , \tag{S22}$$

$$A_C^{kl} \approx -\frac{M_C^{kl}}{\log[(1-\pi_C)(1-\pi_R)\overline{p}_R]} . \tag{S23}$$

The denominators are now simply numbers. The eigenvalues of A_R^{kl} and A_C^{kl} are thus the eigenvalues of the landscape matrices, divided by these numerical factors:

$$\lambda_R \approx -\frac{\lambda_{M_R}}{\log(1-\pi_R)} , \tag{S24}$$

$$\lambda_C \approx -\frac{\lambda_{M_C}}{\log[(1-\pi_C)(1-\pi_R)\overline{p}_R]} , \tag{S25}$$

where λ_{M_i} is the leading eigenvalue of the landscape matrix of species i.

Step 3b: Approximate the average patch occupancies using Eq. S14. In our example, we have $\overline{p}_R \approx 1 - 1/\lambda_R$:

$$\lambda_R \approx -\frac{\lambda_{M_R}}{\log(1-\pi_R)} , \tag{S26}$$

$$\lambda_C \approx -\frac{\lambda_{M_C}}{\log\left[(1-\pi_C)(1-\pi_R)\left(1+\dfrac{\log(1-\pi_R)}{\lambda_{M_R}}\right)\right]} . \tag{S27}$$

Figure S1 visualizes these persistence conditions.

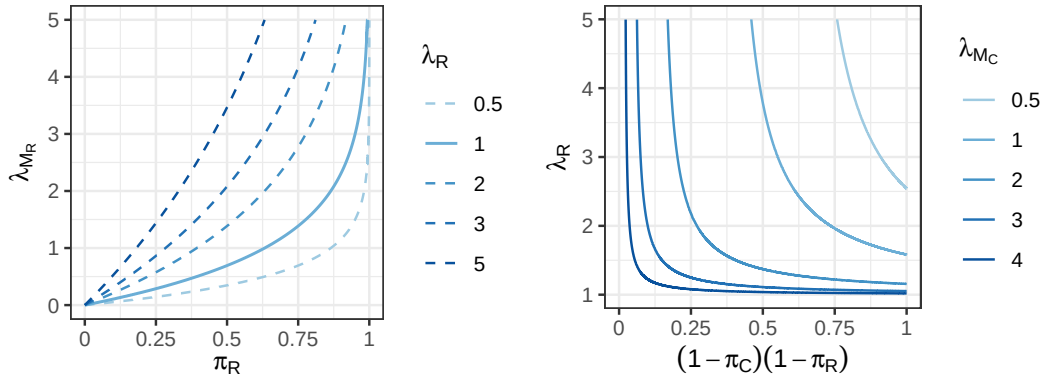

Figure S1: Persistence in the one consumer, one resource system. Left: curves of identical resource metapopulation capacities λ_R (colors), as a function of the resource's baseline extinction probability π_R (abscissa) and the leading eigenvalue of its landscape matrix λ_{M_R} (ordinate). The solid line corresponds to a metapopulation capacity of one; the species persists for combinations of π_R and λ_{M_R} falling above this line on the graph, and goes extinct below this line. Right: curves along which the consumer metapopulation capacity, λ_C, is equal to one, for various values of the leading eigenvalue of its landscape matrix λ_{M_C} (colors), the product of the consumer and resource baseline persistence probabilities (abscissa), and the resource metapopulation capacity λ_R (ordinate). For each value of λ_{M_C}, points above the corresponding line on the graph lead to the consumer's persistence.

S4.2 Food chain

The above can be generalized to trophic chains of arbitrary length. Let there be S species with baseline extinction probabilities π_i^k. Species 1 is basal and is eaten by species 2; species S is a top predator eating species $S-1$; and species $1 < i < S$ eat species $i-1$ and are eaten by species $i+1$.

Step 1: Solve for the extinction probabilities using the Bayesian network approach. The probability of species $i+1$ being extinct can be written as

$$\delta_{i+1}^k = P^k(\neg(i+1)|i)P^k(i) + P^k(\neg(i+1)|\neg i)P^k(\neg i) \; . \tag{S28}$$

Since every species $i > 1$ has exactly one prey, from Eq. S2 we can write $P^k(\neg(i+1)|i) = \pi_{i+1}^k$ and $P^k(\neg(i+1)|\neg i) = 1$:

$$\delta_{i+1}^k = \pi_{i+1}^k P^k(i) + P^k(\neg i) \; . \tag{S29}$$

Using Eq. S9, we have

$$\begin{aligned} \delta_{i+1}^k &= \pi_{i+1}^k(1-\delta_i^k)p_i^k + 1 - (1-\delta_i^k)p_{i-1}^k \\ &= 1 - (1-\pi_{i+1}^k)p_i^k(1-\delta_i^k) \; , \end{aligned} \tag{S30}$$

which is a recursion equation for the δ_i^k with initial condition $\delta_1^k = \pi_1^k$. The recursion can be solved explicitly:

$$\delta_i^k = 1 - (1-\pi_i^k)\prod_{n=1}^{i-1}(1-\pi_n^k)p_n^k \; . \tag{S31}$$

That this is indeed the solution is shown by writing Eq. S31 for $i+1$:

$$\begin{aligned} \delta_{i+1}^k &= 1 - (1-\pi_{i+1}^k)\prod_{n=1}^{i}(1-\pi_n^k)p_n^k \\ &= 1 - (1-\pi_{i+1}^k)p_i^k \underbrace{(1-\pi_i^k)\prod_{n=1}^{i-1}(1-\pi_n^k)p_n^k}_{1-\delta_i^k \text{ (Eq. S31)}} \\ &= 1 - (1-\pi_{i+1}^k)p_i^k(1-\delta_i^k) \; , \end{aligned} \tag{S32}$$

recovering Eq. S30.

For instance, applying Eq. S31 to a tritrophic chain with a resource (R), consumer (C), and top (T) species, we get

$$\delta_R^k = \pi_R^k \; , \tag{S33}$$

$$\delta_C^k = 1 - (1-\pi_C^k)(1-\pi_R^k)p_R^k \; , \tag{S34}$$

$$\delta_T^k = 1 - (1-\pi_T^k)(1-\pi_C^k)(1-\pi_R^k)p_R^k p_C^k \; . \tag{S35}$$

Step 2: Obtain the metapopulation capacity of each species. We first calculate the Jacobian matrix of each species' principal map evaluated at zero, from Eq. S11. Using Eq. S32, we get

$$A_i^{kl} = -\frac{M_i^{kl}}{\log\left[(1-\pi_i^k)\prod_{n=1}^{i-1}(1-\pi_n^k)p_n^k\right]} \tag{S36}$$

for $i > 1$, and $A_1^{kl} = -M_1^{kl}/\log(1-\pi_i^k)$ for the basal species. The metapopulation capacities are the leading eigenvalues λ_i of the matrices A_i^{kl}. They can be computed sequentially, starting from the basal species and moving up the chain. For each species, we obtain its equilibrium patch occupancy distribution p_i^k, for example from Eq. S12. We then use these to compute A_i^{kl} and then λ_i for subsequent species.

Step 3: Approximate metapopulation capacities analytically. Using the nonspatial baseline extinction probabilities (*Step 3a*), we rewrite Eq. S36 as

$$A_i^{kl} \approx -\frac{M_i^{kl}}{\log\left[(1-\pi_i)\prod_{n=1}^{i-1}(1-\pi_n)\overline{p}_n\right]} \,. \tag{S37}$$

If λ_{M_i} is the leading eigenvalue of species i's landscape matrix M_i^{kl}, then

$$\lambda_i \approx -\frac{\lambda_{M_i}}{\log\left[(1-\pi_i)\prod_{n=1}^{i-1}(1-\pi_n)\overline{p}_n\right]} \,. \tag{S38}$$

We can now use Eq. S14 to express the average patch occupancies (*Step 3b*):

$$\lambda_i \approx -\frac{\lambda_{M_i}}{\log\left[(1-\pi_i)\prod_{n=1}^{i-1}(1-\pi_n)(1-1/\lambda_n)\right]} \,. \tag{S39}$$

For λ_{i+1}, this reads

$$\begin{aligned}
\lambda_{i+1} &\approx -\frac{\lambda_{M_{i+1}}}{\log\left[(1-\pi_{i+1})\prod_{n=1}^{i}(1-\pi_n)(1-1/\lambda_n)\right]} \\
&= -\frac{\lambda_{M_{i+1}}}{\log\left[(1-\pi_{i+1})(1-1/\lambda_i)(1-\pi_i)\prod_{n=1}^{i-1}(1-\pi_n)(1-1/\lambda_n)\right]} \\
&= -\frac{\lambda_{M_{i+1}}}{\log[(1-\pi_{i+1})(1-1/\lambda_i)] + \log\left[(1-\pi_i)\prod_{n=1}^{i-1}(1-\pi_n)(1-1/\lambda_n)\right]} \,.
\end{aligned} \tag{S40}$$

The last term in the denominator is $-\lambda_{M_i}/\lambda_i$ by Eq. S39, therefore

$$\lambda_{i+1} \approx -\frac{\lambda_{M_{i+1}}}{\log[(1-\pi_{i+1})(1-1/\lambda_i)] - \lambda_{M_i}/\lambda_i} \,, \tag{S41}$$

and $\lambda_1 = -\lambda_{M_1}/\log(1-\pi_1)$ for the basal species, giving a recursion equation for the metapopulation capacities λ_i. In fact, one can formally say $\lambda_0 = \infty$ (substituting this into Eq. S41 returns the correct λ_1), which biologically translates into our assumption that the resources of basal species (such as light, water, and nutrients) are always available regardless of landscape fragmentation.

To simplify Eq. S41 further, let us assume that the baseline probability of extinction is the same at all trophic levels: $\pi_i \equiv \pi$ for all species. Let us also assume that the landscape matrices of the species are identical: $\lambda_{M_i} \equiv \lambda_M$. Eq. S41 then becomes

$$\lambda_{i+1} \approx \frac{\lambda_M}{\lambda_M/\lambda_i - \log[(1-\pi)(1-1/\lambda_i)]} \,, \tag{S42}$$

with $\lambda_0 = \infty$. The recursion is only meaningful until λ_i drops below 1, meaning that the ith trophic level cannot persist. To put the equation in an even more convenient form, we divide both sides by λ_M and then take reciprocals:

$$\frac{\lambda_M}{\lambda_{i+1}} = \frac{\lambda_M}{\lambda_i} - \log\left[(1-\pi)\left(1-\frac{1}{\lambda_i}\right)\right] \,. \tag{S43}$$

Subtracting λ_M/λ_i from both sides, and introducing the notations $\Lambda_i = 1/\lambda_i$ and $\Lambda_M = 1/\lambda_M$:

$$\frac{\Lambda_{i+1} - \Lambda_i}{\Lambda_M} = -\log[(1-\pi)(1-\Lambda_i)] \,. \tag{S44}$$

Since $\Lambda_i = 1/\lambda_i$ and $\lambda_0 = \infty$, the initial condition for this recursion equation is $\Lambda_0 = 0$; now persistence requires Λ_i to be less than one, and the recursion is only meaningful until Λ_i exceeds 1.

We now show that the sequence of inverse metapopulation capacities Λ_i defined by Eq. S44 is strictly increasing, and it is guaranteed to go above the persistence threshold of 1 at some point (as long as the

baseline extinction probability π is not exactly zero, in which case trophic chains of arbitrary length will trivially be able to persist). Indeed, the right hand side of Eq. S44, measuring the scaled difference between the Λ's of two adjacent trophic levels, is strictly positive: since $(1-\pi)$ is between 0 and 1, and so is $(1-\Lambda_i)$ (because $\Lambda_0 = 0$, and persistence requires $\Lambda_i < 1$), their product is also a number between 0 and 1. The negative log of such a number is a positive number: $-\log[(1-\pi)(1-\Lambda_i)] > 0$. Furthermore, Eq. S44 has no biologically meaningful (positive) fixed point, and therefore the fact that Λ_i increases at every step means it must eventually increase above the persistence threshold of 1. The fixed point Λ^* of S44 is obtained by setting $\Lambda_{i+1} = \Lambda_i = \Lambda^*$:

$$0 = -\log[(1-\pi)(1-\Lambda^*)] \,, \tag{S45}$$

whose unique solution is manifestly negative:

$$\Lambda^* = -\frac{\pi}{1-\pi} < 0 \tag{S46}$$

and therefore lies outside the biologically relevant positive domain.

The fact that the Λ_i must eventually increase above the persistence threshold of 1 imposes a cap on the maximum number of trophic levels. To explore how restrictive this cap is, we consider the limit of a very small Λ_M (large $\lambda_M = 1/\Lambda_M$). In this limit, the left hand side of Eq. S44 approaches the value of a derivative, and it can be approximated as a differential equation:

$$\frac{\mathrm{d}\Lambda(\tau)}{\mathrm{d}\tau} = -\log[(1-\pi)(1-\Lambda(\tau))] \tag{S47}$$

with initial condition $\Lambda(0) = 0$, where $\tau = T\Lambda_M$ is the rescaled trophic level (T is the original one). We ask the question: at what value of the scaled trophic level τ does this equation reach the persistence threshold of $\Lambda(\tau) = 1$?

We can answer this by solving the differential equation. Separating variables and integrating, we get

$$\int \mathrm{d}\tau = -\int \frac{\mathrm{d}\Lambda}{\log[(1-\pi)(1-\Lambda)]} + K \,, \tag{S48}$$

where K is a constant of integration. The integral on the left is simply τ plus a constant; the one on the right can be expressed through the logarithmic integral function $\mathrm{li}(x)$, whose definition is

$$\mathrm{li}(x) = \int_0^x \frac{\mathrm{d}\kappa}{\log(\kappa)} \,. \tag{S49}$$

Using this, we perform the integrals to get

$$\tau = \frac{\mathrm{li}[(1-\pi)(1-\Lambda)]}{1-\pi} + K \,. \tag{S50}$$

The constant K is fixed by substituting $\tau = 0$ above and using the initial condition $\Lambda(0) = 0$:

$$0 = \frac{\mathrm{li}(1-\pi)}{1-\pi} + K \,, \tag{S51}$$

from which

$$K = -\frac{\mathrm{li}(1-\pi)}{1-\pi} \,. \tag{S52}$$

We thus have

$$\tau = \frac{\mathrm{li}[(1-\pi)(1-\Lambda)] - \mathrm{li}(1-\pi)}{1-\pi} \tag{S53}$$

as the solution. Since we are interested in the value of τ at the point when $\Lambda(\tau)$ reaches the threshold of 1, we substitute $\Lambda = 1$ above. This leads to

$$\tau = \frac{\mathrm{li}(0) - \mathrm{li}(1-\pi)}{1-\pi} \,, \tag{S54}$$

but since $\mathrm{li}(0) = 0$ by Eq. S49, we end up with

$$\tau = -\frac{\mathrm{li}(1-\pi)}{1-\pi} \,. \tag{S55}$$

This result can be made even simpler by approximating its right hand side as $-\log(\pi)$ (Figure S2). We then have

$$\tau \approx -\log(\pi) \,. \tag{S56}$$

Changing from the rescaled trophic level $\tau = T\Lambda_M = T/\lambda_M$ to the original T yields the final result:

$$T = -\lambda_M \frac{\mathrm{li}(1-\pi)}{1-\pi} \approx -\lambda_M \log(\pi) \,. \tag{S57}$$

While this was derived assuming that λ_M is large, it is highly accurate for all values of λ_M. This is demonstrated in Figure S3, where the maximum trophic level is first obtained and plotted by directly iterating Eq. S42 until λ_i falls below 1 (left panel), and then by applying $T = -\lambda_M \log(\pi)$ (right panel).

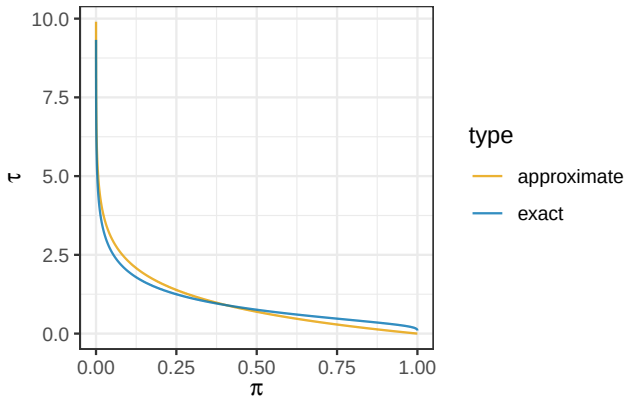

Figure S2: The scaled number of trophic levels $\tau = T/\lambda_M$ against the baseline extinction probability π, given by the exact $\tau = -\mathrm{li}(1-\pi)/(1-\pi)$ (Eq. S55) and the approximate $\tau = -\log(\pi)$ (Eq. S56). For practical purposes, the approximate expression is just as good as the exact one.

Figure S3 also reveals that this maximum number is quite limited unless π is small and λ_M simultaneously large. To get a sense of the typical magnitude of λ_M, we can use the approximation

$$\lambda_M \approx G_D \frac{N}{A} \xi^D \tag{S58}$$

developed by Grilli *et al.* (2015). Here D is the dimensionality of the landscape (in our case $D = 2$), G_D is a numerical factor depending on landscape dimensionality and the shape of the dispersal kernel, N is the number of patches, A the total landscape area, and ξ the characteristic dispersal distance. Using data on three real butterfly metapopulations (Hanski 1994), we estimate λ_M for each of them in Table S1.

In each case, λ_M is in the order of 1. This means that the ordinate of Figure S3 likely captures an empirically relevant range of possible λ_M values. This also implies a potentially quite restricted number of possible trophic levels.

S4.3 One predator with two prey

Let there be two (not necessarily basal) prey species R_i ($i = 1, 2$) with marginal extinction probabilities δ_i^k, and one predator C with a baseline of π_C^k consuming both. The marginal probability of extinction for the consumer is written

$$\begin{aligned} \delta_C^k = {} & P^k(\neg C|R_1R_2)P^k(R_1)P^k(R_2) + P^k(\neg C|\neg R_1R_2)P^k(\neg R_1)P^k(R_2) \\ & + P^k(\neg C|R_1\neg R_2)P^k(R_1)P^k(\neg R_2) + P^k(\neg C|\neg R_1\neg R_2)P^k(\neg R_1)P^k(\neg R_2) \,. \end{aligned} \tag{S59}$$

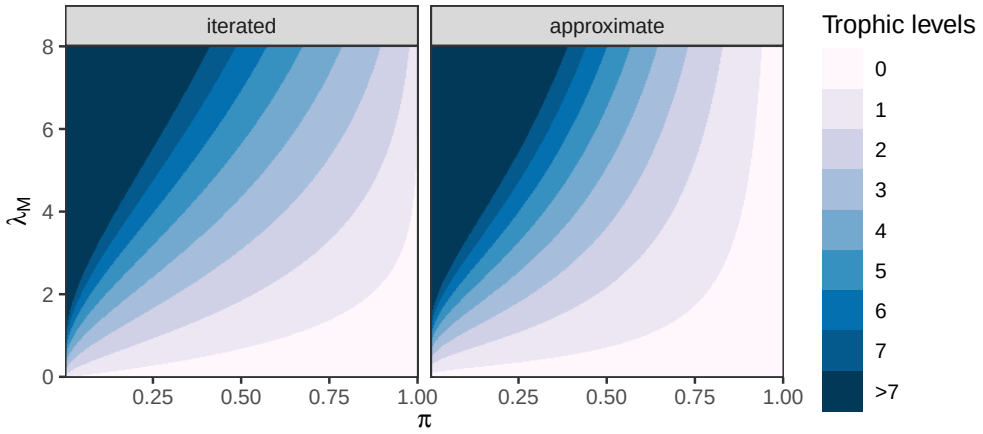

Figure S3: The maximum number of trophic levels, as a function of a common baseline extinction probability π and the leading eigenvalue of a common landscape matrix λ_M. Unless π is low and λ_M high, the metacommunity structure itself puts a cap on the number of possible trophic levels. The left panel is obtained by numerically iterating Eq. S42 until λ_i drops below the persistence threshold of 1. The right panel is based on the simple $T = -\lambda_M \log(\pi)$ of Eq. S57. The approximation matches the actual results well.

species	N	A	ξ	$\lambda_M \approx G_D(N/A)\xi^2$
Melitaea cinxia	50	20	0.5	3.93
Hesperia comma	64	104	0.5	0.97
Scolitantides orion	70	149	0.5	0.74

Table S1: Estimated leading eigenvalues λ_M of the landscape matrices of three butterfly species. Parameters are from Hanski (1994, Table 2). Our ξ is defined as the inverse of the original α; since α was always set to 2, here we use $\xi = 0.5$. The λ_M are approximated using the formula of Grilli *et al.* (2015). For the exponential kernel and $D = 2$, $G_D = 6.283$ (see Grilli *et al.* 2015, Supplementary Information, Section 5 for the derivation). In each case, $\lambda \sim O(1)$, suggesting that the ordinate of Figure S3 covers an empirically relevant region.

Using Eqs. S2 and S9:

$$\begin{aligned}\delta_C^k = {} & \pi_C^k(1-\delta_{R_1}^k)(1-\delta_{R_2}^k)p_{R_1}^k p_{R_2}^k \\ & + \left[\pi_C^k + (1-\pi_C^k)w(1/2)\right]\left[(1-\delta_{R_1}^k)p_{R_1}^k(1-(1-\delta_{R_2}^k)p_{R_2}^k) + (1-\delta_{R_2}^k)p_{R_2}^k(1-(1-\delta_{R_1}^k)p_{R_1})\right] \\ & + (1-(1-\delta_{R_1}^k)p_{R_1}^k)(1-(1-\delta_{R_2}^k)p_{R_2}^k)\,.\end{aligned} \tag{S60}$$

If we further specify $w(1/2) = 1/2$, the above expression simplifies to

$$\delta_C^k = 1-(1-\pi_C^k)\left[\frac{p_{R_1}^k(1-\delta_{R_1}^k) + p_{R_2}^k(1-\delta_{R_2}^k)}{2}\right], \tag{S61}$$

or

$$\delta_C^k = 1-(1-\pi_C^k)\overline{p_R^k(1-\delta_R^k)}\,, \tag{S62}$$

where the overbar denotes the arithmetic average over the prey species R_i. In case the prey are basal, $\delta_{R_i}^k = \pi_{R_i}^k$ and the formula is the same as Eq. S19, with the average replacing the single $p_R^k(1-\pi_R^k)$ term.

S4.4 One predator with multiple prey

Let there be S prey species R_i with marginal extinction probabilities δ_i^k, and one consumer C with baseline π_C^k eating all prey. We propose the following conjecture: assuming $w(f) = f$ in Eq. S2, the consumer's

marginal extinction probability reads

$$\delta_C^k = 1 - (1-\pi_C^k)\overline{p_R^k(1-\delta_R^k)}\,, \tag{S63}$$

where the average is taken over all prey species R_i. Eq. S63 is a direct generalization of Eq. S62 from two to an arbitrary number of prey items.

We prove this conjecture for the case of identical prey ($\delta_i^k \equiv \delta^k$, $p_{R_i}^k \equiv p_R^k$). Using Eq. S1:

$$\begin{aligned}
\delta_C^k = {} & P^k(\neg C|R_1R_2\ldots R_S)\underbrace{P^k(R_1)P^k(R_2)\cdots P^k(R_S)}_{[P^k(R)]^S \text{ [since } P^k(R_i)\equiv P^k(R)]} \\
& + SP^k(\neg C|\neg R_1R_2\ldots R_S)\underbrace{P^k(\neg R_1)P^k(R_2)\cdots P^k(R_S)}_{(1-P^k(R))P^k(R)^{S-1}} \\
& + \binom{S}{2}P^k(\neg C|\neg R_1\neg R_2\ldots R_S)\underbrace{P^k(\neg R_1)P^k(\neg R_2)\cdots P^k(R_S)}_{(1-P^k(R))^2P^k(R)^{S-2}} \\
& + \cdots \\
& + SP^k(\neg C|R_1\neg R_2\ldots \neg R_S)\underbrace{P^k(R_1)P^k(\neg R_2)\cdots P^k(\neg R_S)}_{(1-P^k(R))^{S-1}P^k(R)} \\
& + P^k(\neg C|\neg R_1\neg R_2\ldots \neg R_S)\underbrace{P^k(\neg R_1)P^k(\neg R_2)\cdots P^k(\neg R_S)}_{(1-P^k(R))^S}\,.
\end{aligned} \tag{S64}$$

We used the fact that $P^k(\neg C|\neg R_1R_2R_3\ldots) = P^k(\neg C|R_1\neg R_2R_3\ldots)$ and so on, since the prey are equivalent. Using the notation $P^k(\neg C|k)$ for the probability of C being extinct given that k of its resources are absent, we can rewrite the above as

$$\begin{aligned}
\delta_C^k = {} & P^k(\neg C|0)(1-P^k(R))^0P^k(R)^S \\
& + SP^k(\neg C|1)(b_R^k)^1P^k(R)^{S-1} \\
& + \binom{S}{2}P^k(\neg C|2)(1-P^k(R))^2P^k(R)^{S-2} \\
& + \cdots \\
& + SP^k(\neg C|S-1)(1-P^k(R))^{S-1}P^k(R)^1 \\
& + P^k(\neg C|S)(1-P^k(R))^SP^k(R)^0,
\end{aligned} \tag{S65}$$

which is compactly written as

$$\delta_C^k = \sum_{n=0}^{S}\binom{S}{n}P^k(\neg C|n)(1-P^k(R))^nP^k(R)^{S-n}. \tag{S66}$$

Since we use the linear response function $w(f) = f$, and $f = n/S$ is the fraction of resources absent, $P^k(\neg C|n)$ can be written as $\pi_C^k + (1-\pi_C^k)(n/S)$ (Eq. S2):

$$\begin{aligned}
\delta_C^k = P^k(\neg C) &= \sum_{n=0}^{S}\binom{S}{n}\left[\pi_C^k + (1-\pi_C^k)\frac{n}{S}\right](1-P^k(R))^nP^k(R)^{S-n} \\
&= \pi_C^k\underbrace{\sum_{n=0}^{S}\binom{S}{n}(1-P^k(R))^nP^k(R)^{S-n}}_{1} + \frac{1-\pi_C^k}{S}\underbrace{\sum_{n=0}^{S}n\binom{S}{n}(1-P^k(R))^nP^k(R)^{S-n}}_{S(1-P^k(R))}.
\end{aligned} \tag{S67}$$

The first sum is over the binomial distribution and therefore equal to 1; the second sum is over n times the binomial distribution and is therefore equal to its mean, $S\pi_R^k$. We therefore end up with

$\delta_C^k = \pi_C^k + (1-\pi_C^k)(1-P^k(R))$. Substituting $P^k(R) = p_R^k(1-\delta_R^k)$ (Eq. S9) and rearranging, we recover Eq. S63.

Though a strict proof is missing, the formula held true even for non-equivalent prey species, without exception. We therefore proceed by assuming that Eq. S63 holds for this general case as well, even though we emphasize that this is not yet strictly proven.

S4.5 Two strict trophic levels

Consider S basal prey species $R_1,\ldots,R_S$, and L consumers $C_1,\ldots,C_S$. For the prey, $\delta_{R_i}^k = \pi_{R_i}^k$. Let $\mathcal{P}(A,B,\ldots)$ denote the set of prey jointly consumed by species A, B, ... To determine the marginal extinction probabilities of the consumers, we can apply the argument of Section S4.4 to each consumer species individually:

$$\delta_{C_i}^k = 1-(1-\pi_{C_i}^k)\overline{p_{\mathcal{P}(C_i)}^k(1-\delta_{\mathcal{P}(C_i)}^k)}\,, \tag{S68}$$

where the arithmetic average is taken over the set of C_i's prey, $\mathcal{P}(C_i)$.

S4.6 Multispecies trophic chain

In this case we have several trophic levels, each with a certain number of species, and species at a given level can only consume species from one level below. Eq. S68 holds for any two trophic levels, so it can be used recursively to find the marginal extinction probabilities of any species, starting from the basal level where for each basal species i, we have $\delta_i^k = \pi_i^k$. For another species i on the second level, applying Eq. S68 yields

$$\delta_i^k = 1-(1-\pi_i^k)\overline{p_{\mathcal{P}(i)}^k(1-\pi_{\mathcal{P}(i)}^k)}\,, \tag{S69}$$

and for the third,

$$\delta_i^k = 1-(1-\pi_i^k)\overline{p_{\mathcal{P}(i)}^k(1-\pi_{\mathcal{P}(i)}^k)\overline{p_{\mathcal{P}(\mathcal{P}(i))}^k(1-\pi_{\mathcal{P}(\mathcal{P}(i))}^k)}}\,. \tag{S70}$$

Here the the higher overbar averages over the prey (on level 2) of the focal species i, while the lower overbar averages over the prey (on level 1) of those consumers (on level 2) that are eaten by i. The notation $\mathcal{P}(\mathcal{P}(i))$ reads "the prey items of the set of species which are prey items of species i".

S4.7 Simple omnivory module

Let there be a single basal resource R, a consumer C eating the resource, and a top species T eating both the consumer and the resource. We assume $w(f) = f$.

Step 1: Solve for the extinction probabilities using the Bayesian network approach. The basal and consumer species are the same as they were in Section S4.1, so their probabilities are given by Eqs. S18 and S19. For the top species, we write

$$\begin{aligned}\delta_T^k = {} & P^k(\neg T|RC)P^k(R)P^k(C) + P^k(\neg T|\neg RC)P^k(\neg R)P^k(C) \\ & + P^k(\neg T|R\neg C)P^k(R)P^k(\neg C) + P^k(\neg T|\neg R\neg C)P^k(\neg R)P^k(\neg C)\,.\end{aligned} \tag{S71}$$

Using Eq. S2 with $w(f) = f$:

$$\begin{aligned}\delta_T^k &= \pi_T^k P^k(R)P^k(C) + \left(\frac{1+\pi_T^k}{2}\right)\Big[P^k(R)(1-P^k(C)+P^k(C)(1-P^k(R)))\Big] + (1-P^k(C))(1-P^k(R)) \\ &= 1-\frac{1}{2}(1-\pi_T^k)\Big[P^k(R)+P^k(C)\Big]\,.\end{aligned} \tag{S72}$$

Applying Eq. S9 and Eqs. S18-S19 for the resource and consumer:

$$\delta_T^k = 1-\frac{1}{2}(1-\pi_T^k)\Big[(1-\pi_R^k)p_R^k + (1-\pi_C^k)(1-\pi_R^k)p_C^k p_R^k\Big]\,, \tag{S73}$$

or, after simplifying,

$$\delta_T^k = 1-(1-\pi_T^k)\left(\frac{1+p_C^k(1-\pi_C^k)}{2}\right)(1-\pi_R^k)p_R^k\,. \tag{S74}$$

Writing out the probabilities for all three species:

$$\delta_R^k = \pi_R^k\,, \tag{S75}$$

$$\delta_C^k = 1-(1-\pi_C^k)(1-\pi_R^k)p_R^k\,, \tag{S76}$$

$$\delta_T^k = 1-(1-\pi_T^k)\left(\frac{1+p_C^k(1-\pi_C^k)}{2}\right)(1-\pi_R^k)p_R^k\,. \tag{S77}$$

Comparing these results with Eqs. S33-S35, we see that the only difference is in δ_T^k: in the omnivory scenario, $(1-\pi_C^k)p_C^k$ is replaced by $(1+(1-\pi_C^k)p_C^k)/2$. Since $(1-\pi_C^k)p_C^k$ is the product of two probabilities, it is between 0 and 1. But then, $(1+(1-\pi_C^k)p_C^k)/2 > (1-\pi_C^k)p_C^k$ holds, and so δ_T^k in the omnivory case is always lower than δ_T^k in the corresponding food chain scenario—a result in line with common sense.

Step 2: Obtain the metapopulation capacity of each species. The Jacobian matrices of the principal maps evaluated at zero, from Eq. S11, read

$$A_R^{kl} = -\frac{M_R^{kl}}{\log(1-\pi_R^k)}\,, \tag{S78}$$

$$A_C^{kl} = -\frac{M_C^{kl}}{\log[(1-\pi_C^k)(1-\pi_R^k)p_R^k]}\,, \tag{S79}$$

$$A_T^{kl} = -\frac{M_T^{kl}}{\log\left[(1-\pi_T^k)\left(1+p_C^k(1-\pi_C^k)\right)(1-\pi_R^k)p_R^k/2\right]}\,. \tag{S80}$$

The metapopulation capacities are the leading eigenvalues of the three matrices above.

Step 3: Approximate metapopulation capacities analytically. Using the nonspatial baseline extinction probabilities and average patch occupancies (*Step 3a*):

$$A_R^{kl} \approx -\frac{M_R^{kl}}{\log(1-\pi_R)}\,, \tag{S81}$$

$$A_C^{kl} \approx -\frac{M_C^{kl}}{\log[(1-\pi_C)(1-\pi_R)\overline{p}_R]}\,, \tag{S82}$$

$$A_T^{kl} \approx -\frac{M_T^{kl}}{\log[(1-\pi_T)(1+\overline{p}_C(1-\pi_C))(1-\pi_R)\overline{p}_R/2]}\,, \tag{S83}$$

with leading eigenvalues

$$\lambda_R \approx -\frac{\lambda_{M_R}}{\log(1-\pi_R)}\,, \tag{S84}$$

$$\lambda_C \approx -\frac{\lambda_{M_C}}{\log[(1-\pi_C)(1-\pi_R)\overline{p}_R]}\,, \tag{S85}$$

$$\lambda_T \approx -\frac{\lambda_{M_T}}{\log[(1-\pi_T)(1+\overline{p}_C(1-\pi_C))(1-\pi_R)\overline{p}_R/2]}\,, \tag{S86}$$

$$\tag{S87}$$

where λ_{M_i} is the leading eigenvalue of the ith landscape matrix M_i^{kl}. Using Eq. S14 (*Step 3b*):

$$\lambda_R \approx -\frac{\lambda_{M_R}}{\log(1-\pi_R)}\,, \tag{S88}$$

$$\lambda_C \approx -\frac{\lambda_{M_C}}{\log\left[(1-\pi_C)(1-\pi_R)\left(1+\frac{\log(1-\pi_R)}{\lambda_{M_R}}\right)\right]}\,, \tag{S89}$$

$$\lambda_T \approx -\frac{\lambda_{M_T}}{\log\left[\frac{(1-\pi_R)(1-\pi_T)\left[\lambda_{M_R}+\log(1-\pi_R)\right]\left[(2-\pi_C)\lambda_{M_C}+(1-\pi_C)\log\left[\frac{1-\pi_C(1-\pi_R)\left(\lambda_{M_R}+\log(1-\pi_R)\right)}{\lambda_{M_R}}\right]\right]}{2\lambda_{M_C}\lambda_{M_R}}\right]}\,. \tag{S90}$$

S5 Food webs under habitat loss

S5.1 Generating model food webs

We generated food webs (adjacency matrices of who eats whom) based on the allometric framework of Schneider *et al.* (2016). This topological network model is an extension of the niche model (Williams & Martinez 2000) and accounts for allometric degree distributions and known scaling relationships between species' body mass and trophic level (Riede *et al.* 2011). Each species i is characterized by its average adult body mass m_i. We uniformly sample $\log_{10}$ body masses of S_C consumer species from the interval $[2,12]$, and of S_B basal species from $[0,6]$. Given these body masses, the probability L_{ij} that consumer i has a feeding link to species j is given by

$$L_{ij} = \left[\frac{1}{R_{\text{opt}}}\frac{m_i}{m_j}\exp\left(1-\frac{1}{R_{\text{opt}}}\frac{m_i}{m_j}\right)\right]^{\gamma} \tag{S91}$$

(Schneider *et al.* 2016), where $R_{\text{opt}} = 100$ is the body mass ratio between consumers and their prey that yields the maximum probability of predation (the "optimal" ratio, from the point of view of the consumer), and $\gamma = 2$ is the width of the function (the range of body masses likely eaten by consumers). Of all the webs generated by this method, we only kept those that were acyclic, as this is required by the Bayesian network approach.

S5.2 Trophic levels

The prey-averaged trophic level T_i of species i is defined as

$$T_i = 1 + \sum_{j=1}^{S} T_j B_{ji} \tag{S92}$$

(Williams & Martinez 2004). Here B_{ij} is the $(i,j)$the entry of the food web's adjacency matrix, divided by the number of prey items of species i. In matrix notation, $\mathbf{T} = \mathbf{e} + \mathbf{T}\mathbf{B}^{\mathrm{T}}$, where $\mathbf{e}$ is the vector of all 1's, and $\mathbf{B}^{\mathrm{T}}$ is the transpose of $\mathbf{B}$. We solve for the vector of trophic levels $\mathbf{T}$:

$$\mathbf{T} = \left(\mathbf{I} - \mathbf{B}^{\mathrm{T}}\right)^{-1}\mathbf{e}\,, \tag{S93}$$

$\mathbf{I}$ being the identity matrix. For the purposes of creating figures, we then grouped species based on the nearest half-integer value to their trophic level T_i.

S6 Supplementary model results

S6.1 Removing patches based on the patch value rankings of basal species

Patch removal proceeds as described in the main text.

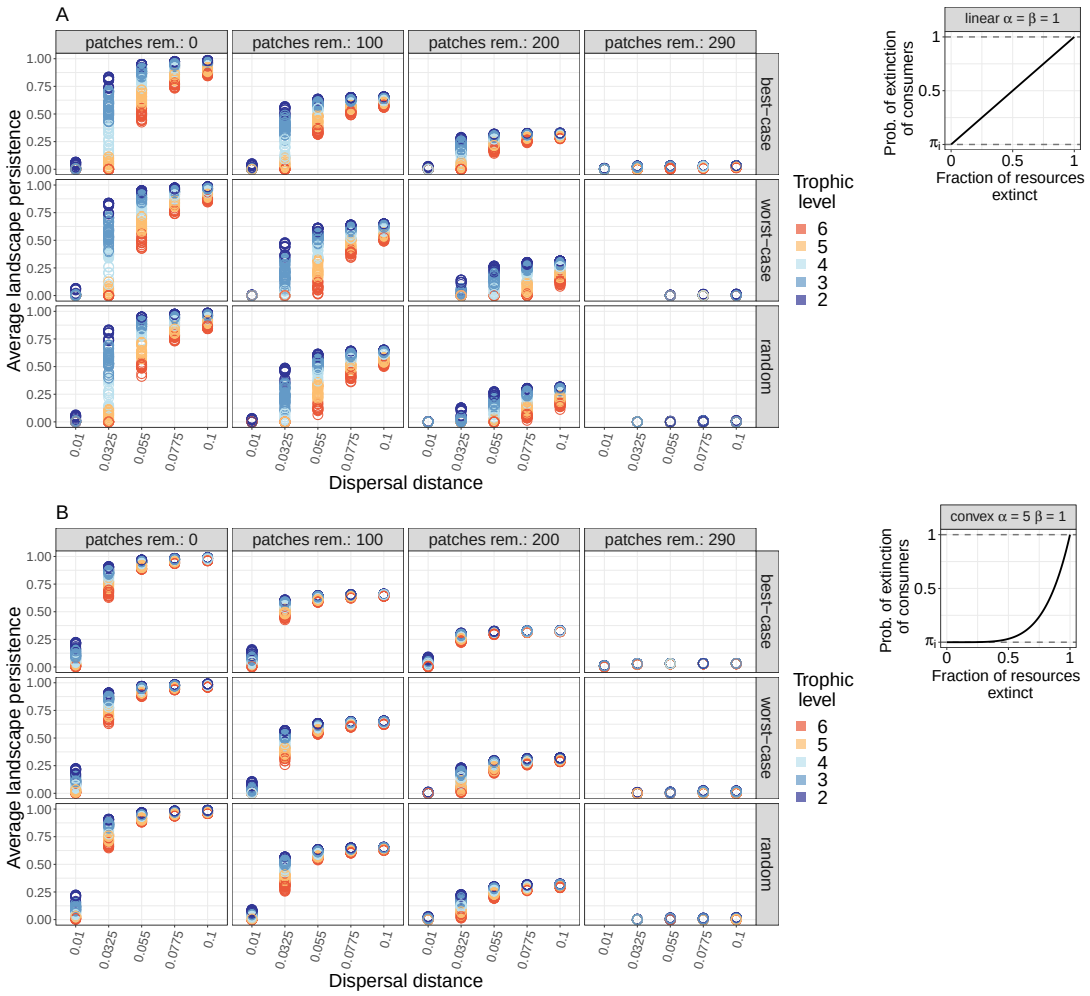

Figure S4: Average species persistence against dispersal distance, in a model food web with 300 consumer and 100 basal species. Average persistence of species i is measured by $\sum_{k=1}^{N} p_i^k/N$, with the understanding that N is the number of patches over the unperturbed landscape and $p_i^k = 0$ on removed patches. A-D are for different functional forms of a consumer's response to the loss of resources (top right insets). Species are grouped into trophic levels (color legends). Rows indicate patch-removal scenario (best-case, worst-case, and random); columns the number of patches removed from the full landscape. Baseline extinction probabilities π_i increase with trophic level (trophic level-based, TLB) and dispersal distances ξ_i range between between 0.01 and 0.1, having the same value across all species in any one parameterization.

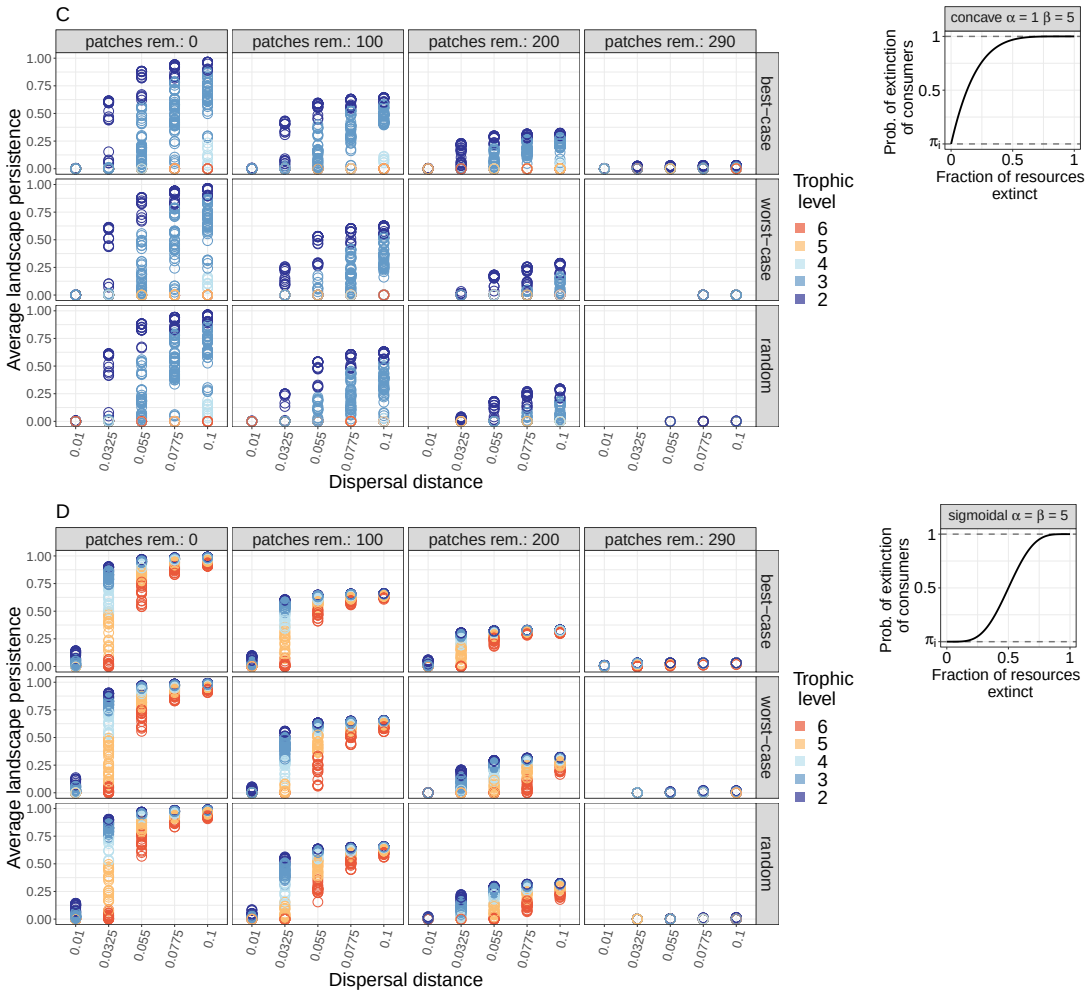

Figure S4: Figure continued.

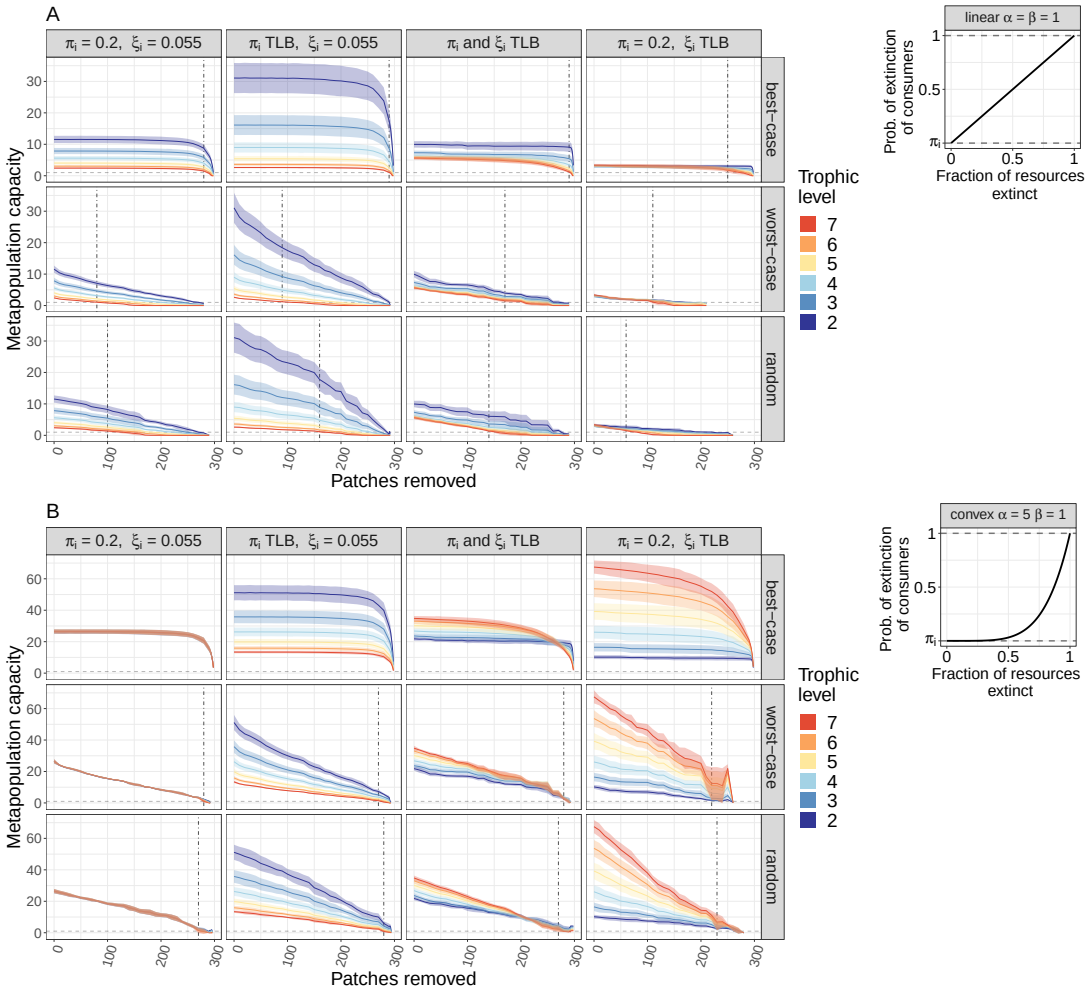

Figure S5: Effect of habitat loss on species persistence in a model food web with 350 consumer and 50 basal species. A-D are for different functional forms of a consumer's response to the loss of resources (top right insets). Species are grouped into trophic levels (color legends); lines show the mean and the bands around them the one standard deviation range of the metapopulation capacities of species in the corresponding trophic level. Rows indicate patch-removal scenario (best-case, worst-case, and random); columns the parameterization method: baseline extinction probabilities π_i and dispersal distances ξ_i can either take on one value across all species, or increase with trophic level (trophic level-based, TLB). Horizontal dashed lines highlight a metapopulation capacity of 1, the threshold for long-term species persistence. Vertical dashed lines show when the metapopulation capacity of the top species in the food web drops below this threshold.

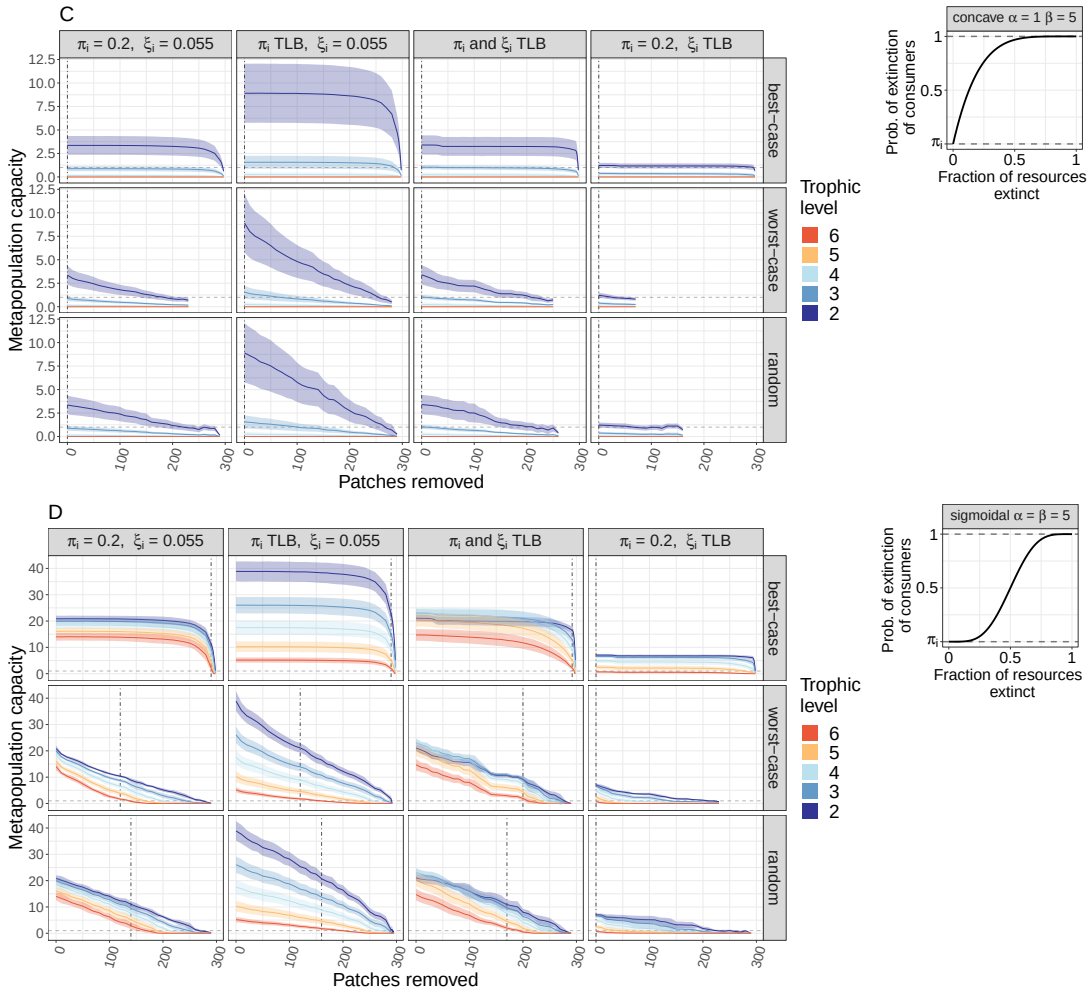

Figure S5: Figure continued.

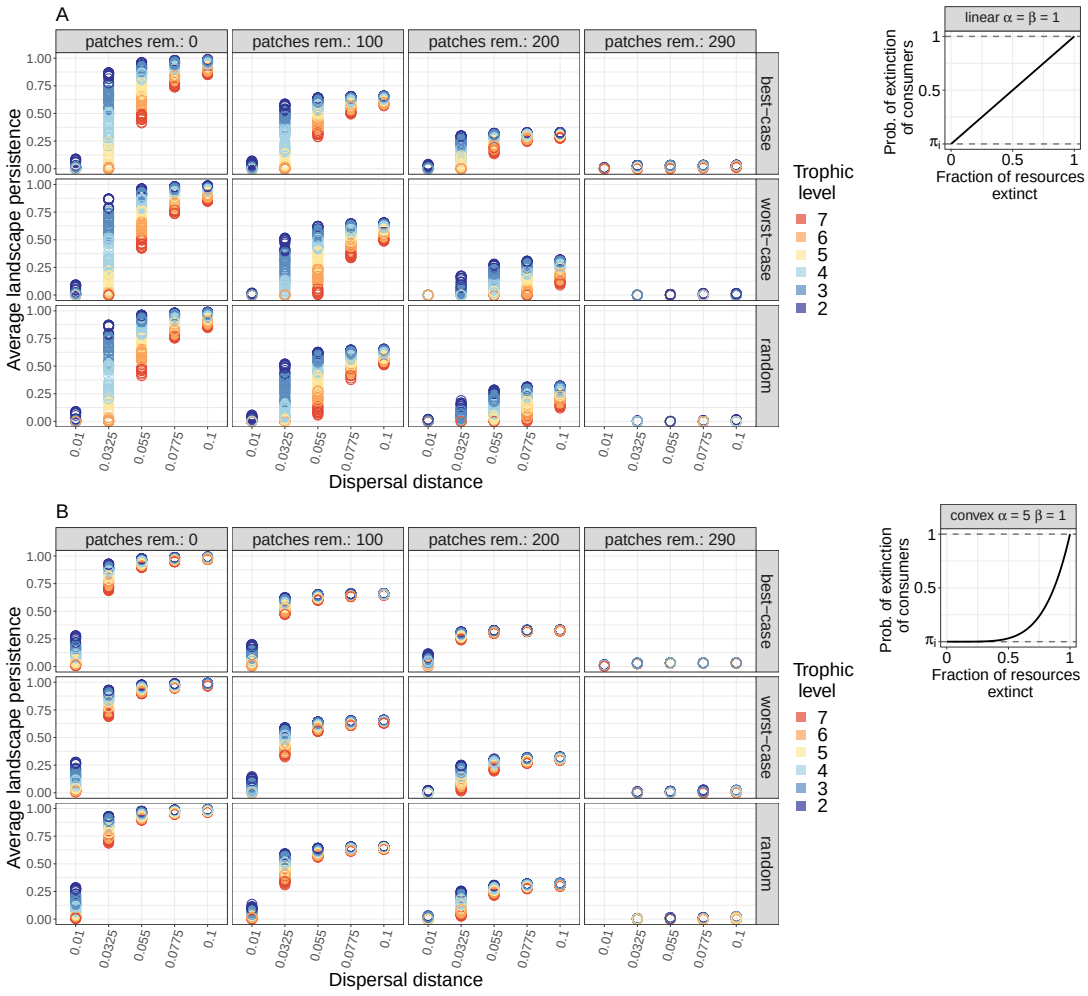

Figure S6: As Figure S4, but with 350 consumer and 50 basal species.

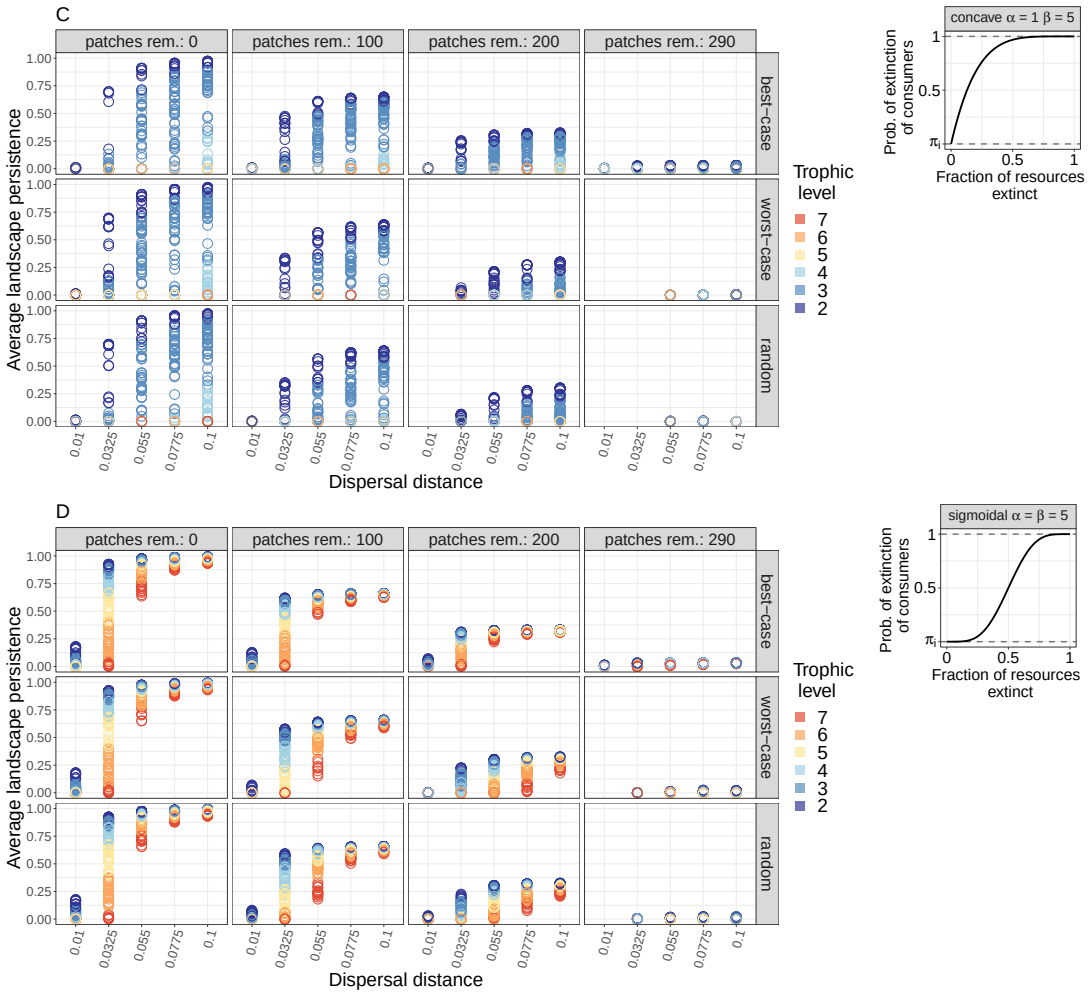

Figure S6: Figure continued.

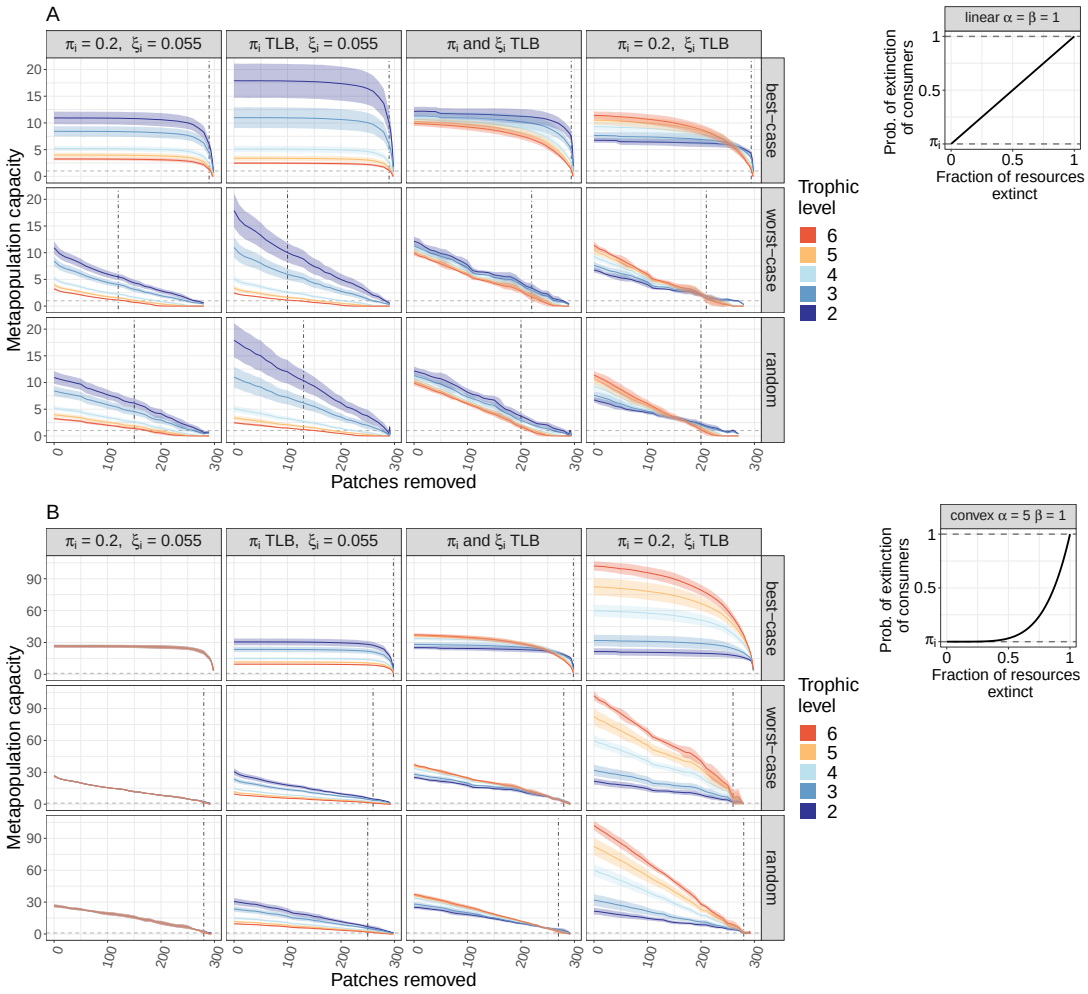

Figure S7: As Figure S5, but with 250 consumer and 150 basal species.

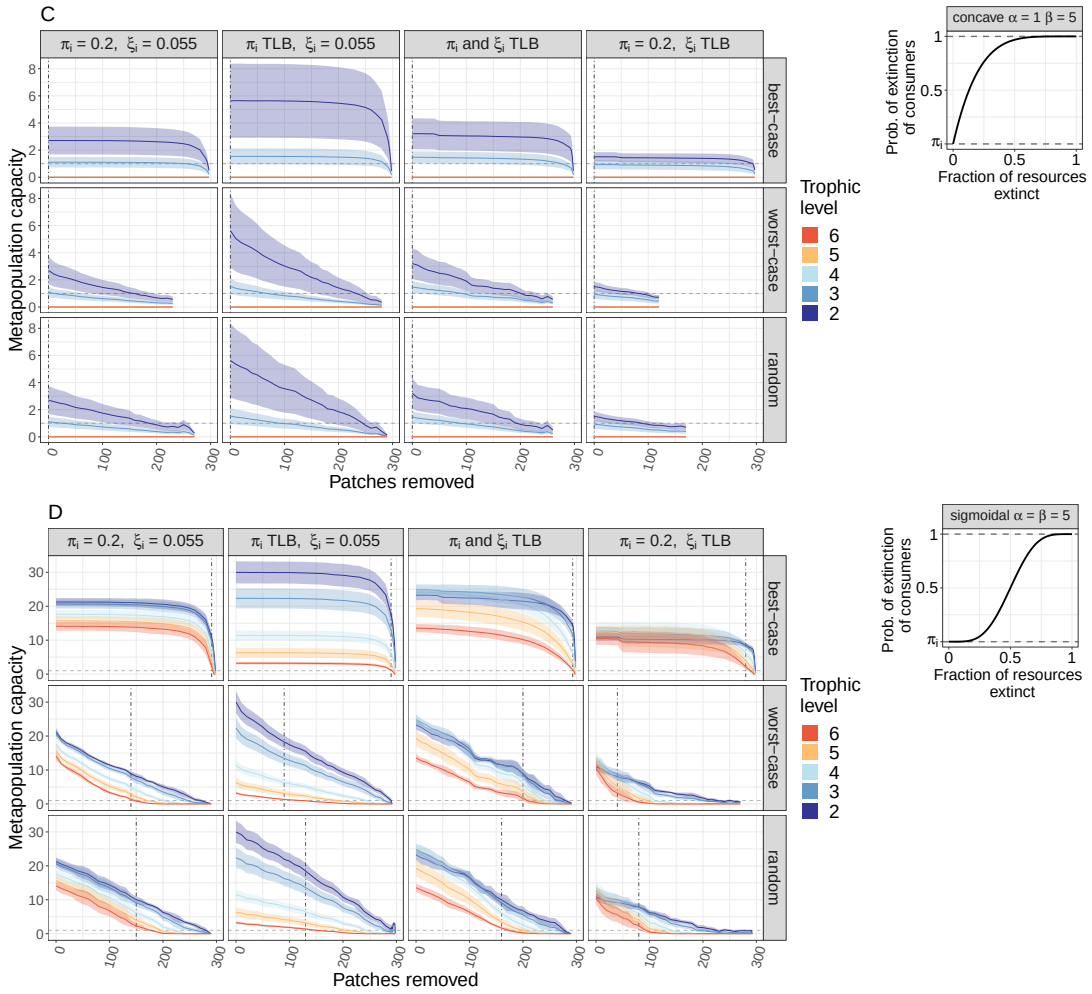

Figure S7: Figure continued.

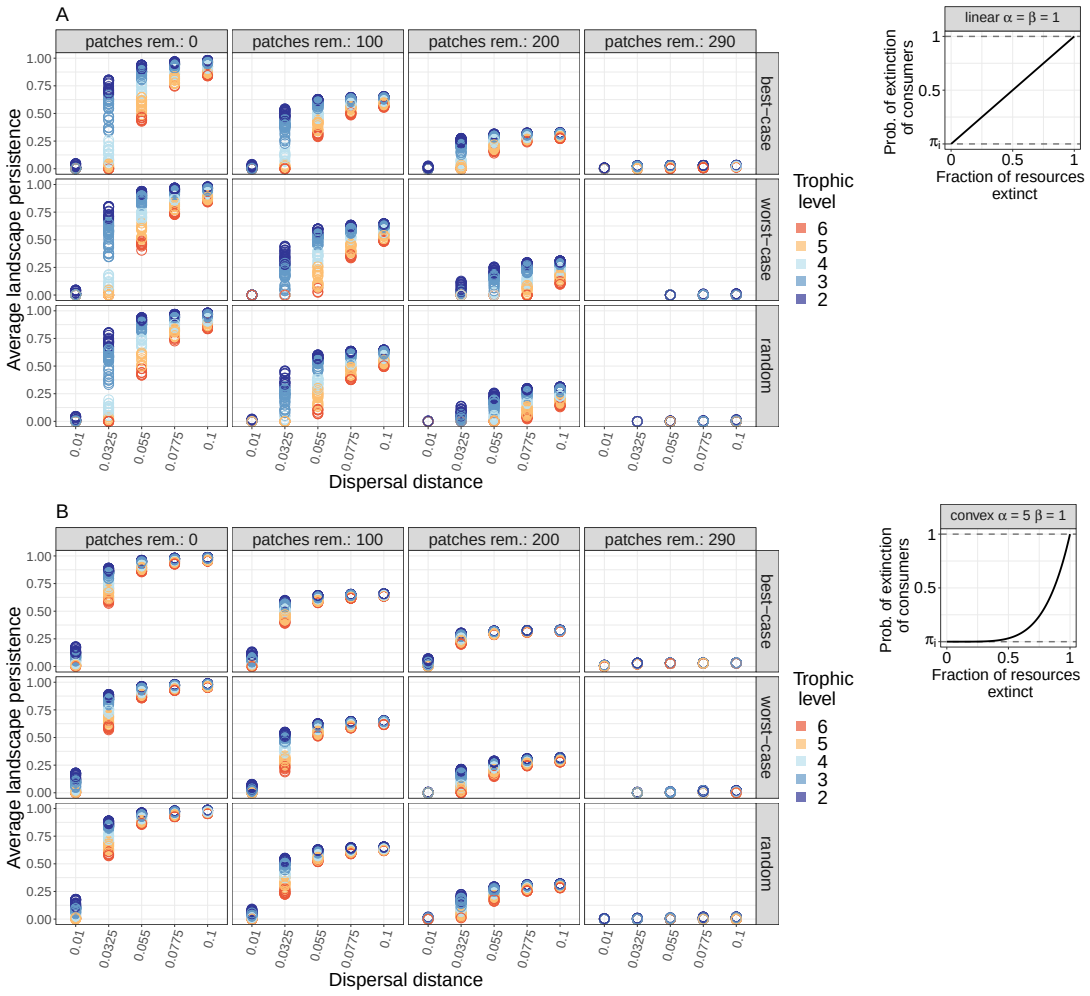

Figure S8: As Figure S4, but with 250 consumer and 150 basal species.

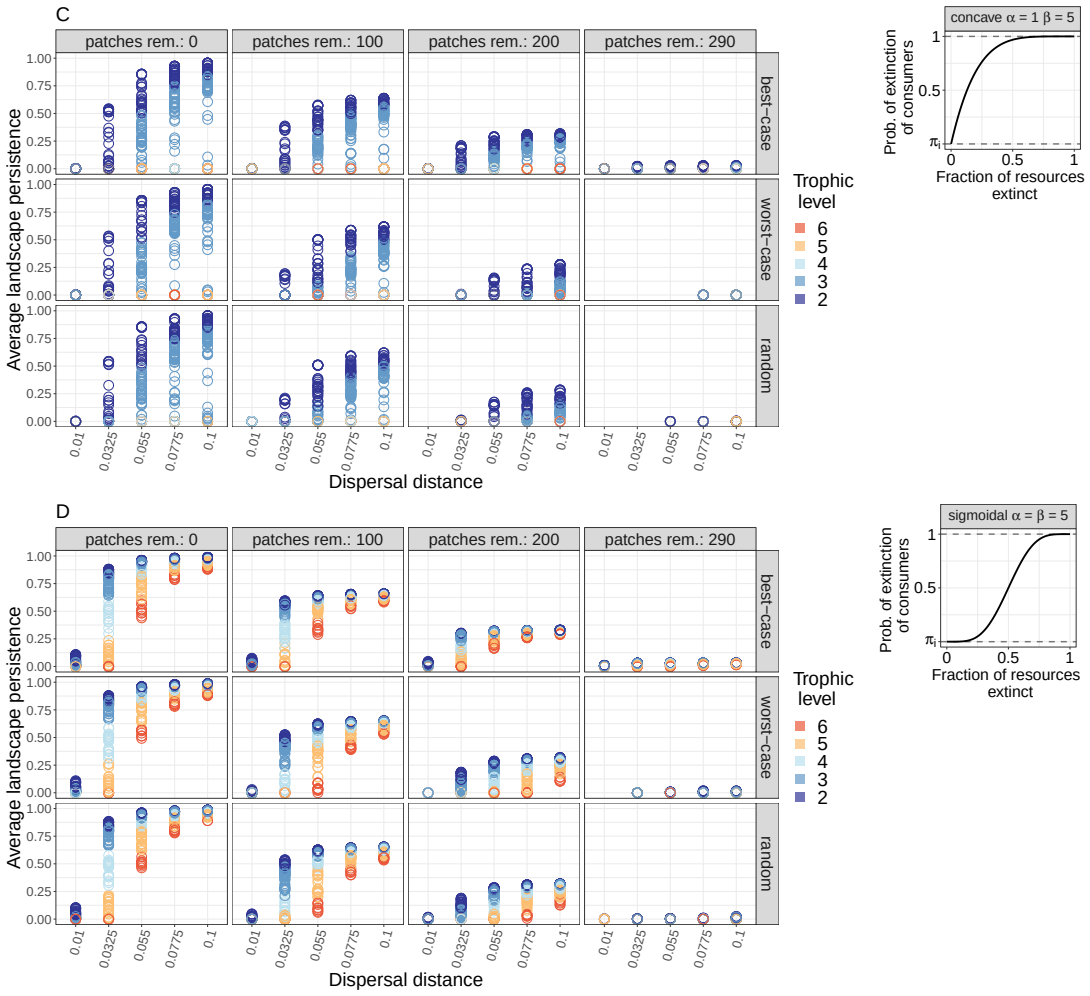

Figure S8: Figure continued.

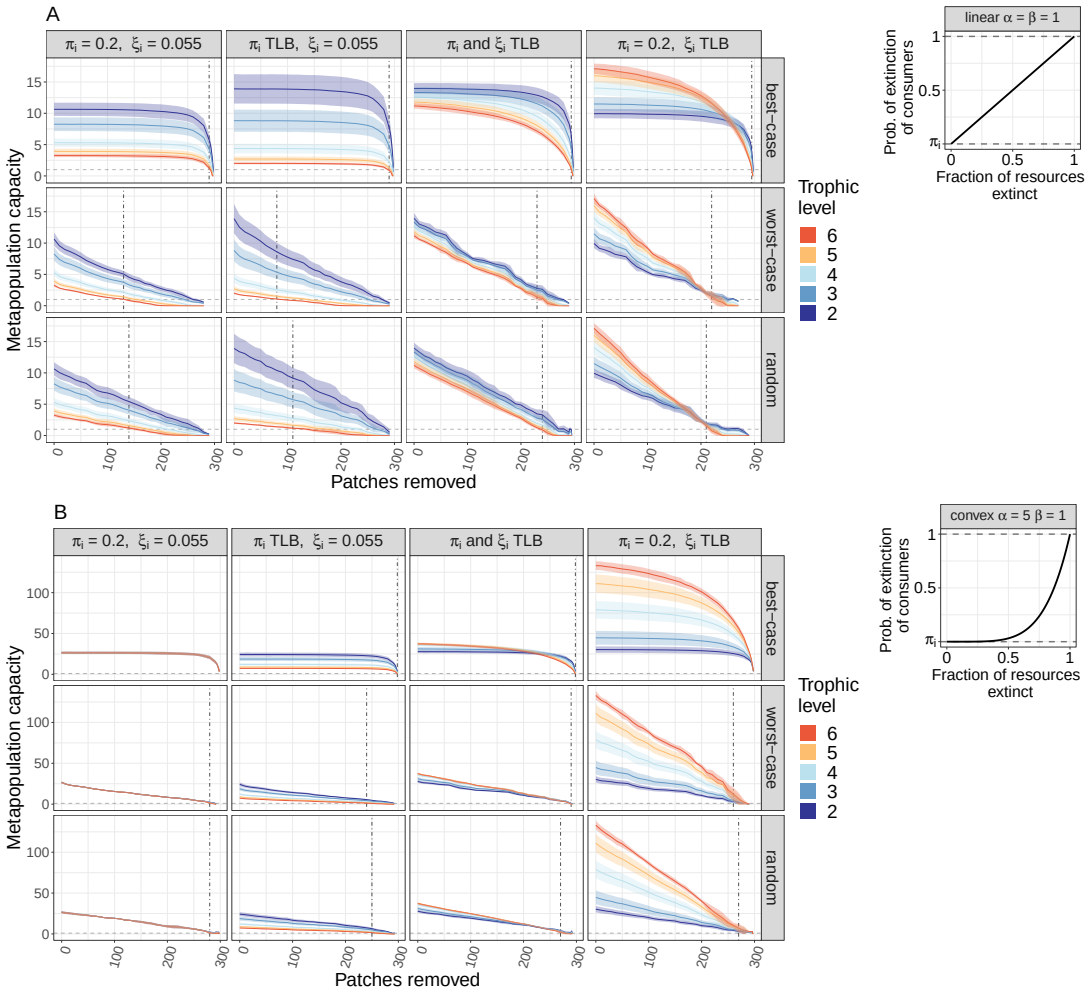

Figure S9: As Figure S5, but with 200 consumer and 200 basal species.

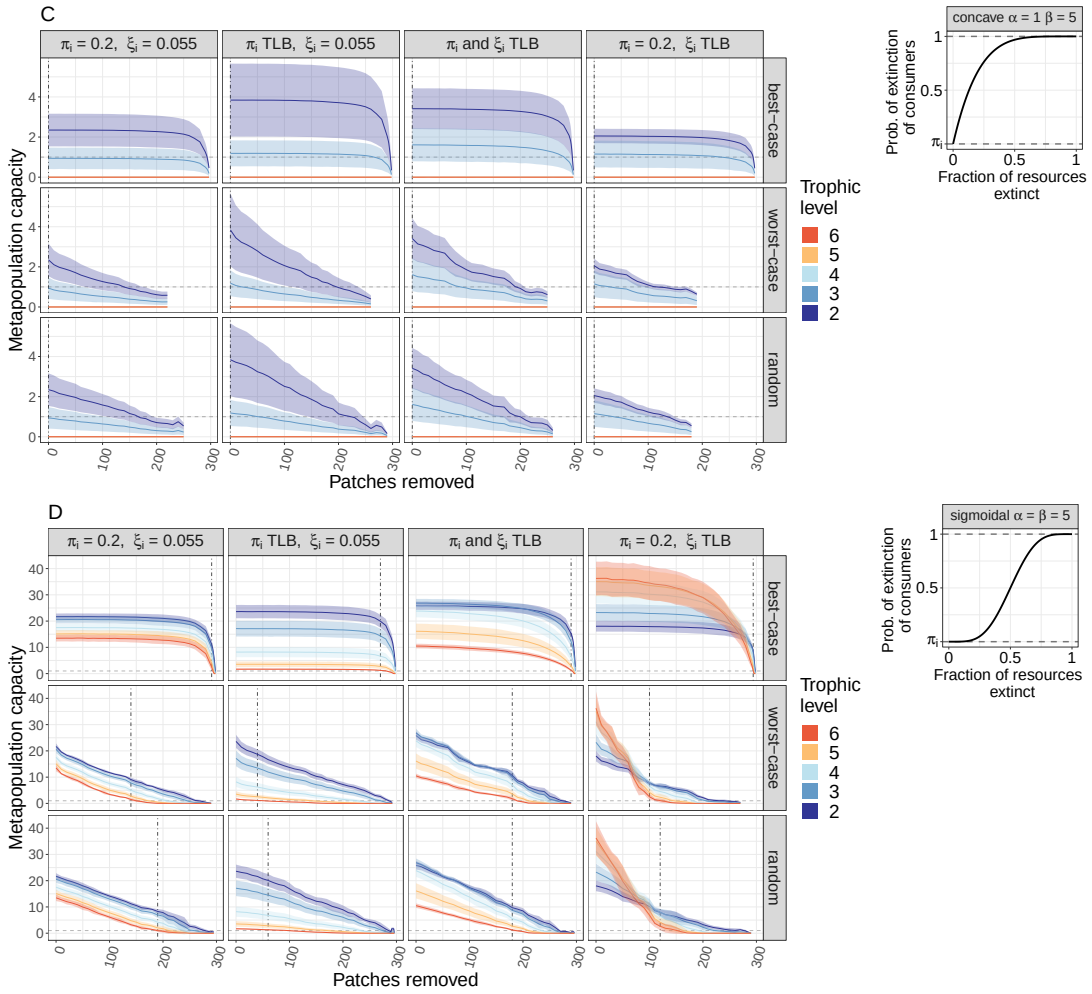

Figure S9: Figure continued.

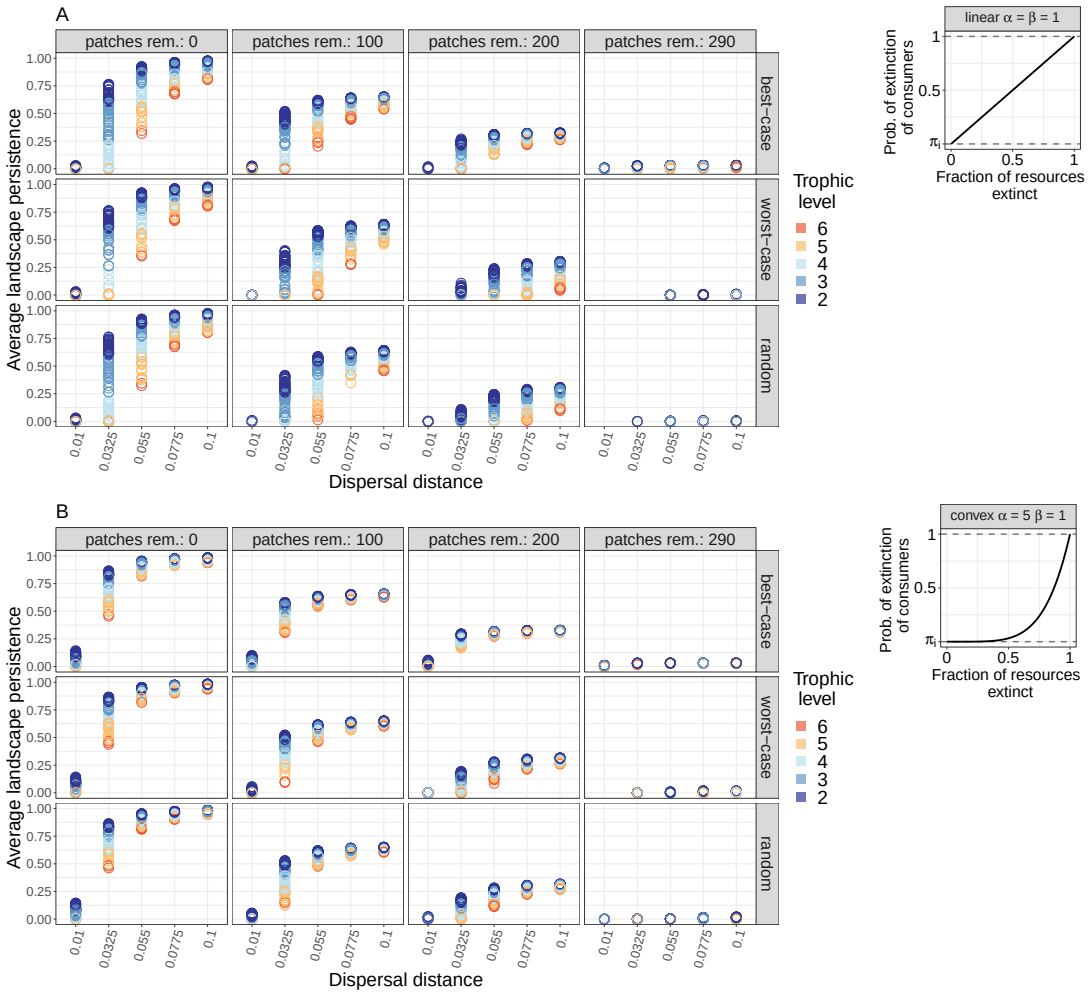

Figure S10: As Figure S4, but with 200 consumer and 200 basal species.

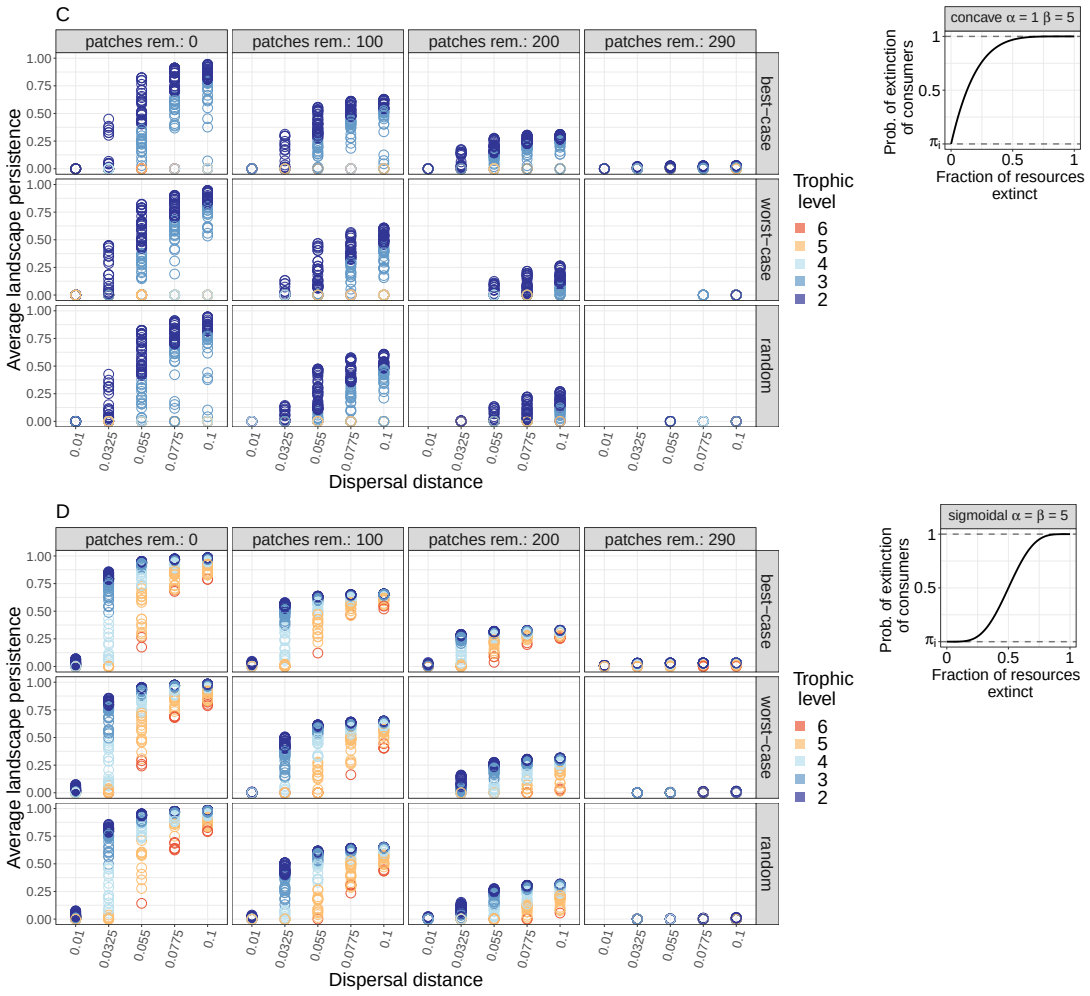

Figure S10: Figure continued.

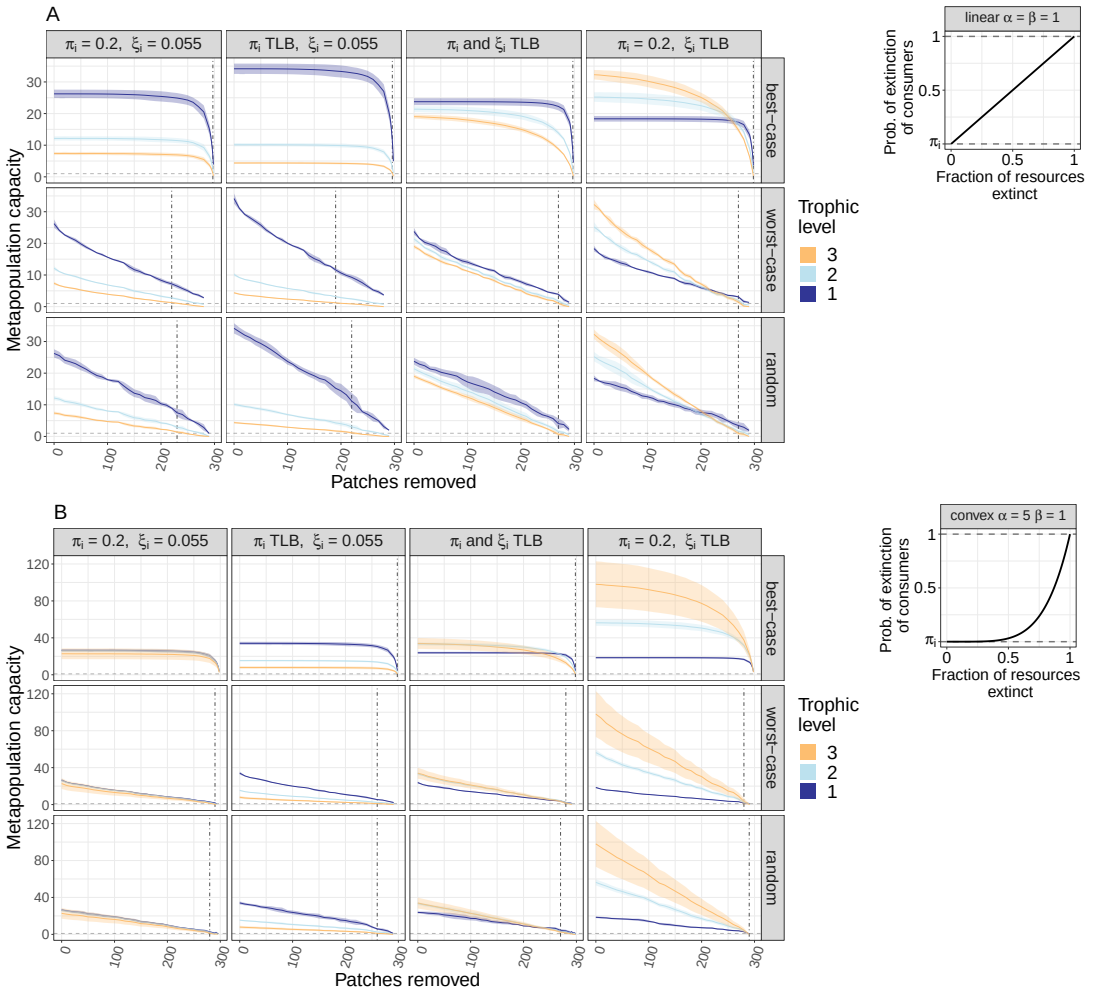

Figure S11: As Figure S5, but for the Serengeti food web.

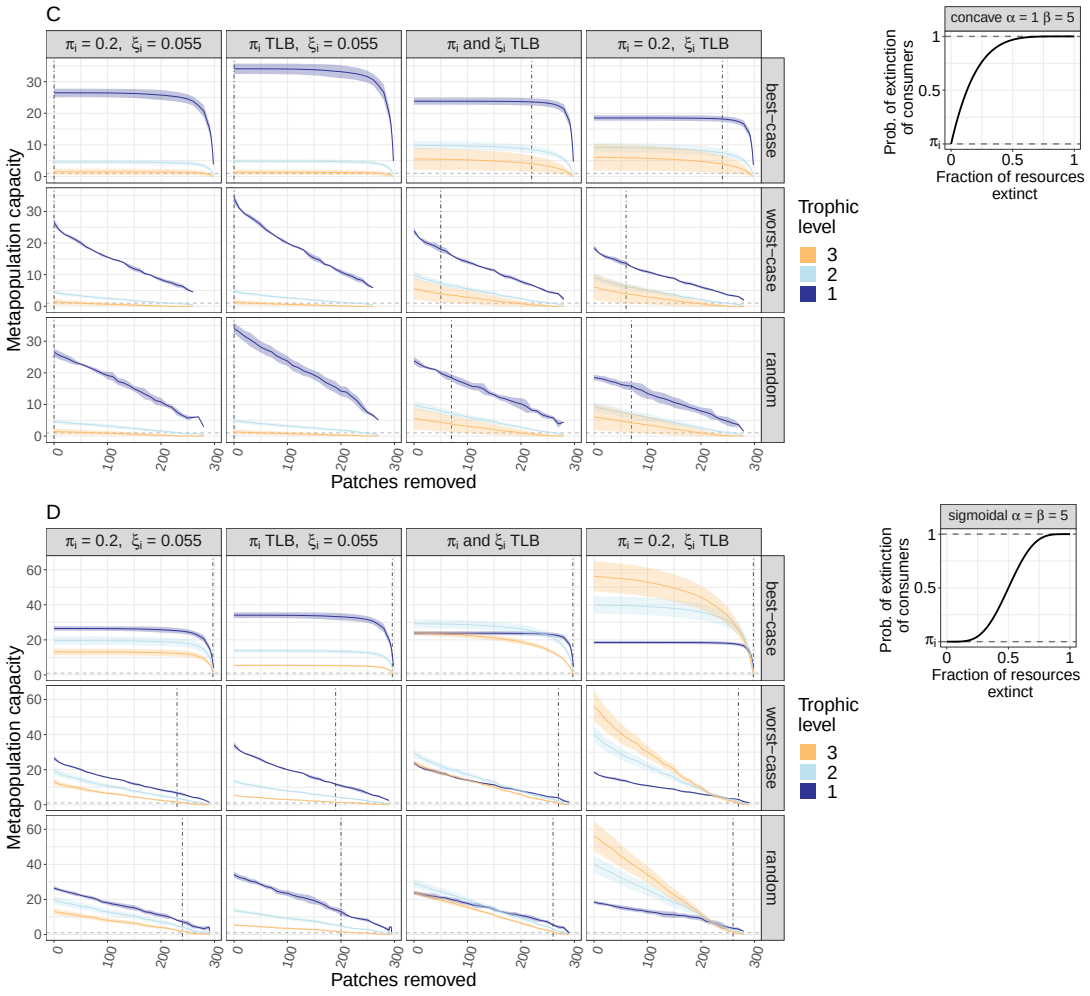

Figure S11: Figure continued.

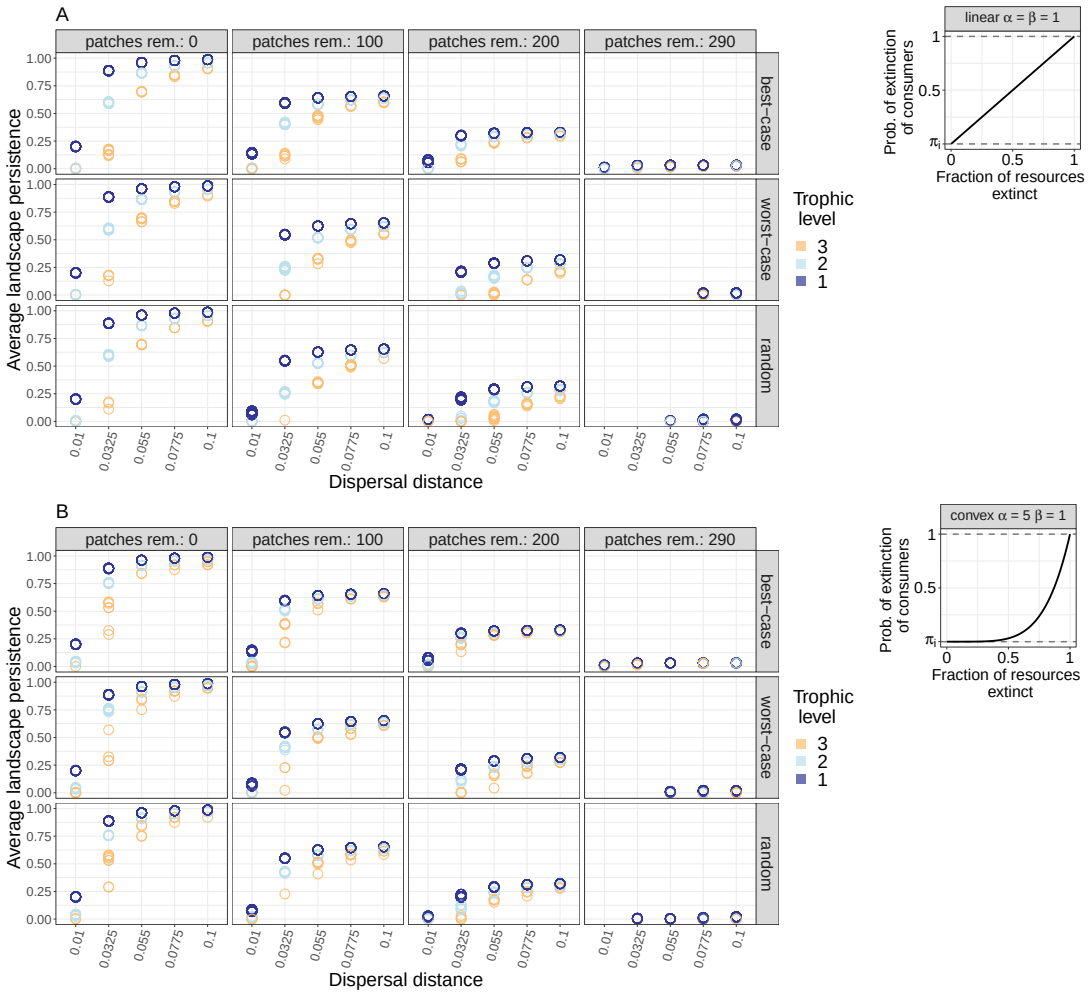

Figure S12: As Figure S4, but for the Serengeti food web.

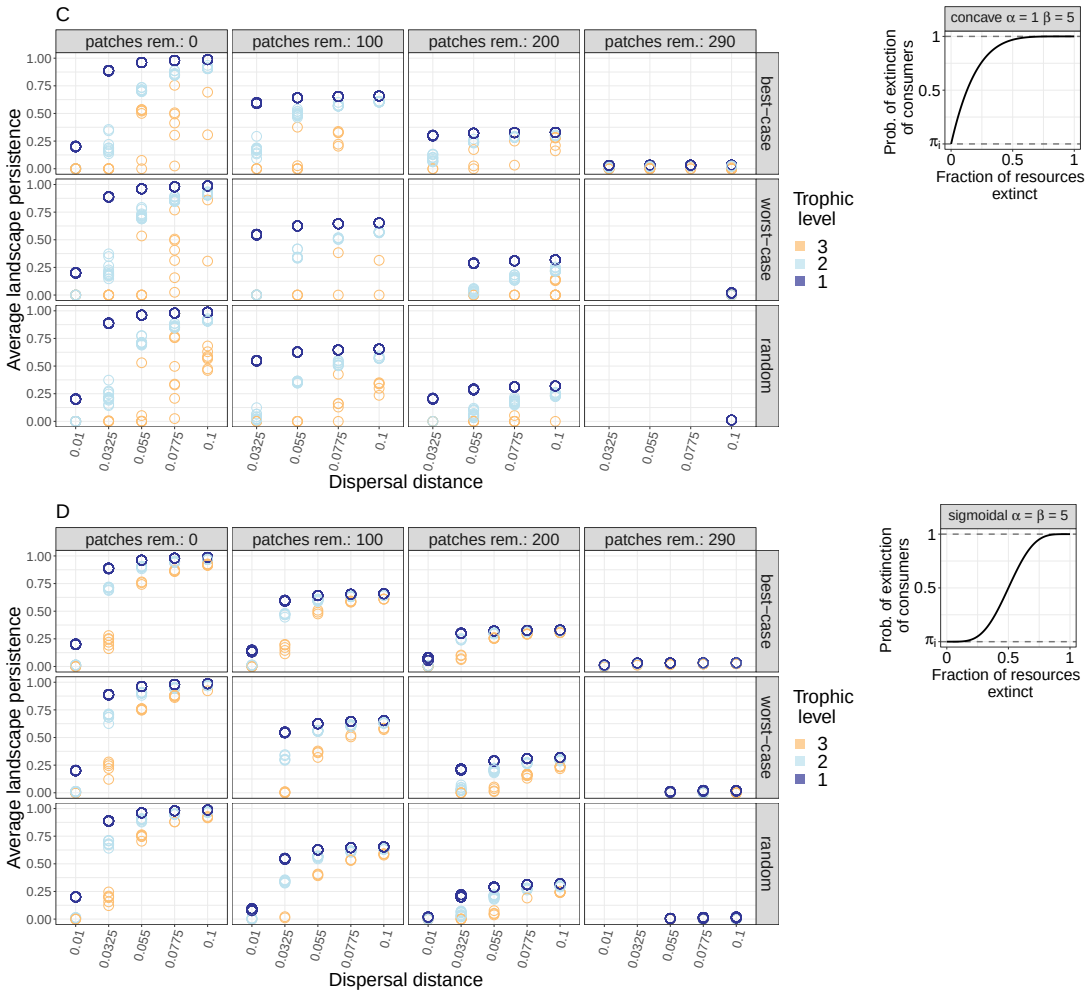

Figure S12: Figure continued.

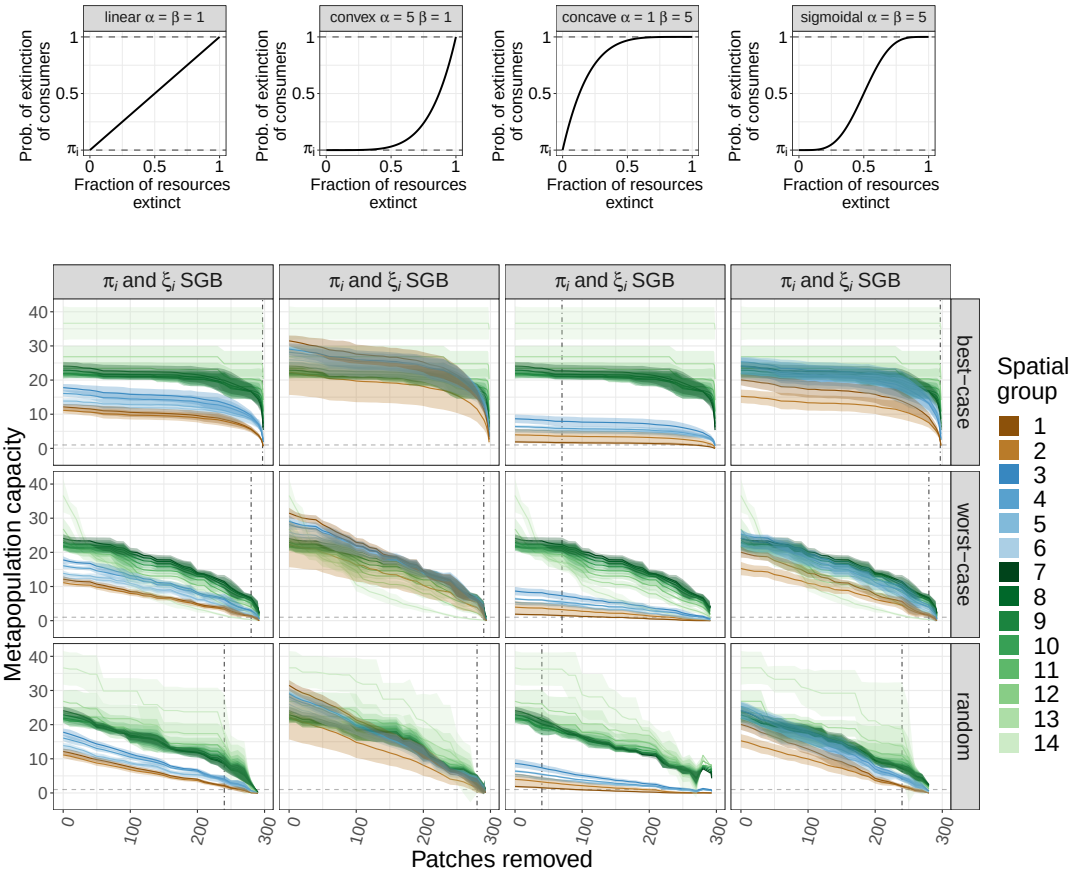

Figure S13: As Figure 4 in the main text, except the species whose metapopulation capacity serves as the basis of patch removal is different. In the main text, this species was the Gum arabic tree (*Acacia senegal*), the sole representative of spatial group 12. Here, we have instead chosen a species from spatial group 14, *Boscia augustifolia*. Results are qualitatively unchanged by this alteration.

S6.2 Removing patches based on the patch value rankings of top species

For the linear functional form of a consumer's response to the loss of resources, we additionally looked at removing patches based on the patch value rankings of top species, instead of basal ones. This means that patch removal was stopped whenever the top species have gone extinct. In case of the Serengeti food web, we removed patches based on the patch value rankings of the leopard (*Panthera pardus*).

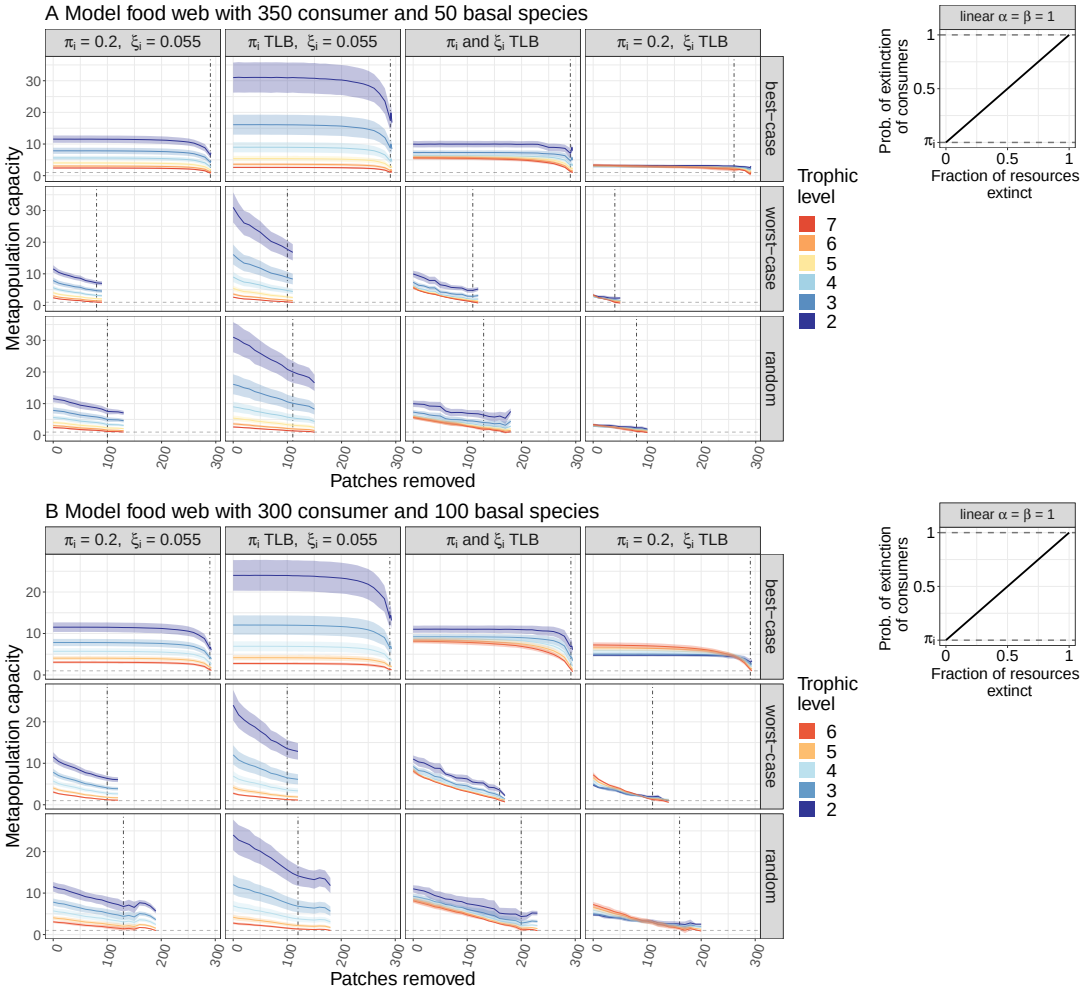

Figure S14: As Figure S5, but patch removal is based on the patch value rankings of top species, and only the linear consumer response to resource loss is implemented (top right insets). Here A-D are for model food webs with different numbers of consumer and basal species and E is for the Serengeti food web.

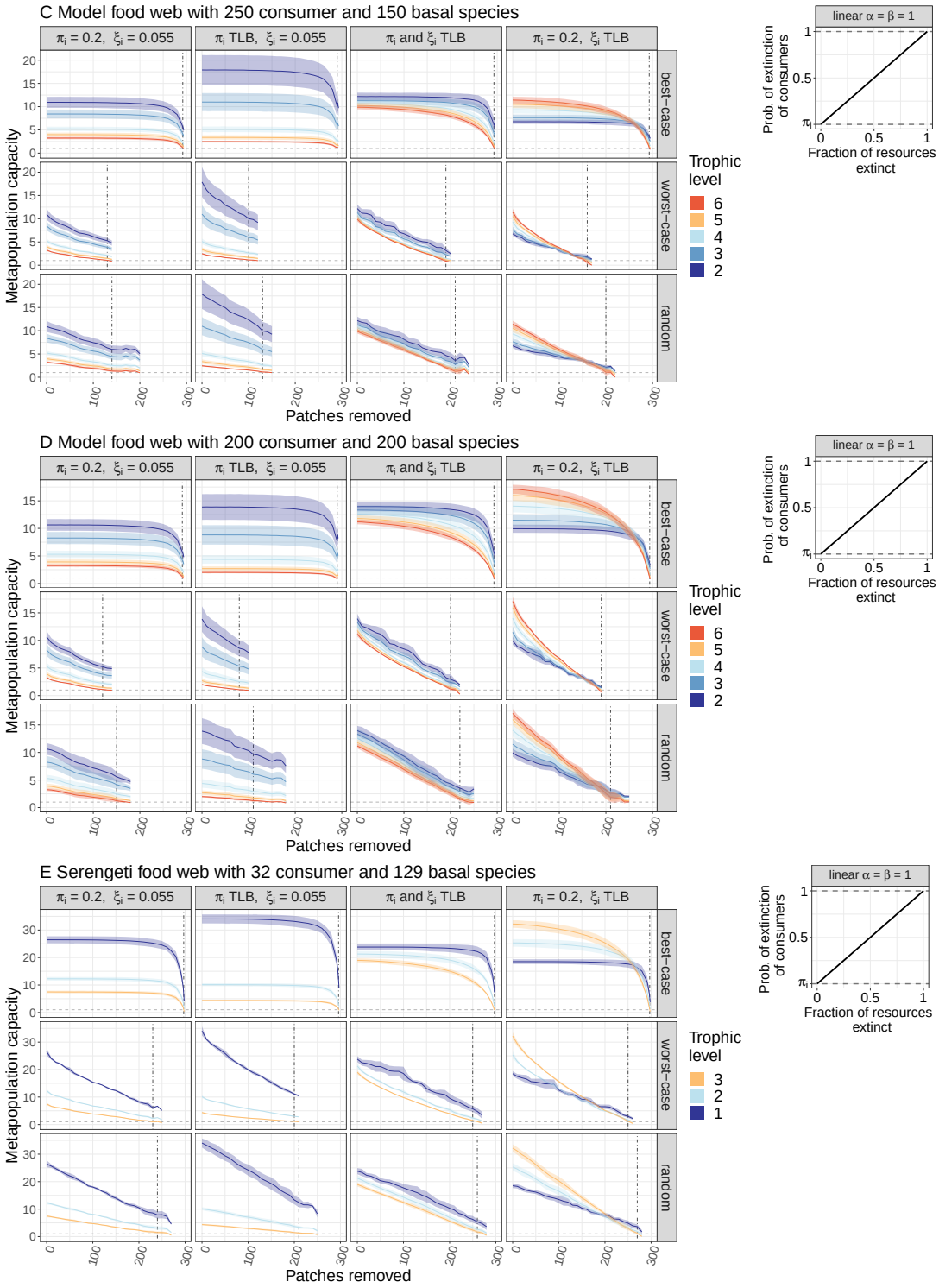

Figure S14: Figure continued.

S7 Assigning different weights to prey species in contributing to their predators' extinction risk

So far, we have made the conditional extinction probability of consumers a function of the fraction of their prey items lost, regardless of the identity of those prey (Eq. S2). Here we relax this assumption by also accounting for the relative contribution of each prey to the predator's diet. Let J_{ji} be the contribution of resource i to the diet of consumer species j. We then define the weighted fraction f' of j's resources lost via

$$f' = \frac{\sum_{j \in \text{absent}} J_{ji}}{\sum_{j \in \text{all prey}} J_{ji}} , \tag{S94}$$

with the sum in the numerator going over prey that are absent, and the one in the denominator over all prey items of the consumer. So f' is the fraction of resources lost weighted for their importance. With this definition, Eq. S2 still holds, but we replace f with f':

$$P(\neg C|f') = \pi_C + (1-\pi_C)w(f') . \tag{S95}$$

We determine the J_{ji} from a matrix of biomass flows at equilibrium. which we obtain as the Jacobian matrix evaluated at equilibrium (the community matrix) of the Allometric Trophic Network model (Section S5.1, Schneider *et al.* 2016), which we have also used to generate our non-weighted trophic networks earlier.

Repeating the patch removal analysis for such a weighted version of our model food web with 50 basal and 350 consumer species, we get Figure S15. This is qualitatively identical to Figure S5, which used the same setup but with non-weighted fractions of prey used (Eq. S2). This shows that the results are robust to relaxing the assumption that species contribute equally to consumers' diets.

S8 The maximum number of trophic levels as a function of landscape size and connectivity

Based on a fully-fledged dynamical model of spatial food webs, Ryser *et al.* (2019) estimated the maximum number of trophic levels that can persist given the average patch distance and the number of patches of a landscape. We have re-created their result (which is summarized in Figure S2 in Ryser *et al.* 2019) using our Bayesian network approach. The results are in Figure S16. They are qualitatively unchanged, with the maximum possible trophic level exhibiting a strong dependence of the maximum attainable trophic level on the spatial scale, and a weaker one on the number of patches.

Our approach can even be used to get a deeper, analytical understanding of this result. Approximating trophic networks as trophic chains, assuming a common baseline extinction probability $\pi_i = \pi$, and using the patch-averaging method described in Section S4.2, we have $T \approx -\lambda_M \log(\pi)$, where T is the maximum number of trophic levels and λ_M is the dominant eigenvalue of the dispersal matrix (Eq. S57). Obtaining these eigenvalues for each of the landscapes used in Figure S16, we depict this approximation in Figure S17. This figure strongly resembles Figure S2 in Ryser *et al.* (2019), and it is based on the fully tractable approximation $T \approx -\lambda_M \log(\pi)$. This lends further credence to the idea that the pattern observed here and in Ryser *et al.* (2019) is not contingent on model details, but is a robust logical consequence of combining trophic interactions and metacommunity structure.

S9 The effect of removing the links between patches

Instead of removing patches in a given sequence (best-case, worst-case, random), we may do the same with the links connecting those patches. This is tantamount to assuming that, instead of habitat destruction, it is the surrounding matrix that gets eroded or destroyed, making it impossible for individuals to travel between patches. We remove links between pairs of patches, meaning that if the link from patch A to patch B is removed, then so is the link from B to A.

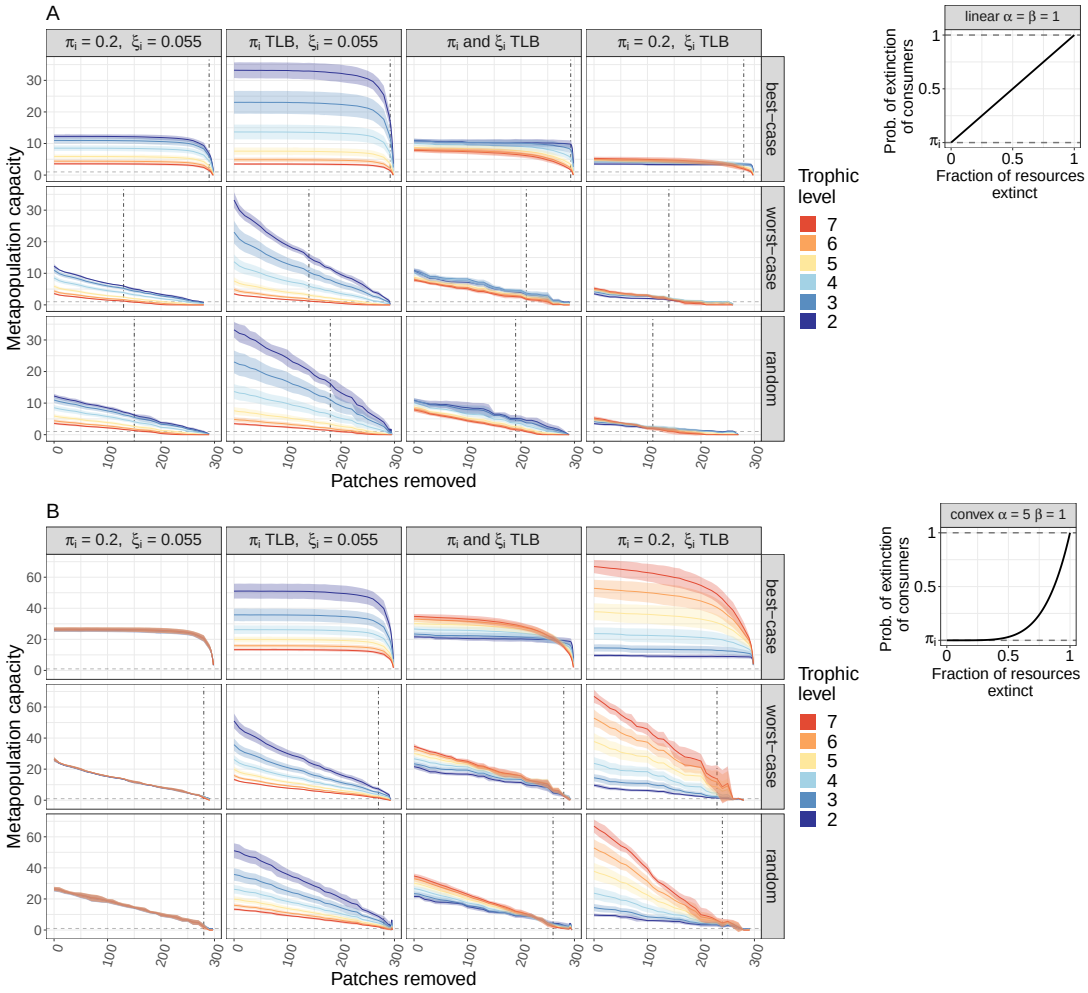

Figure S15: As Figure S5, but with a weighted food web. Results are qualitatively unchanged compared with the non-weighted case.

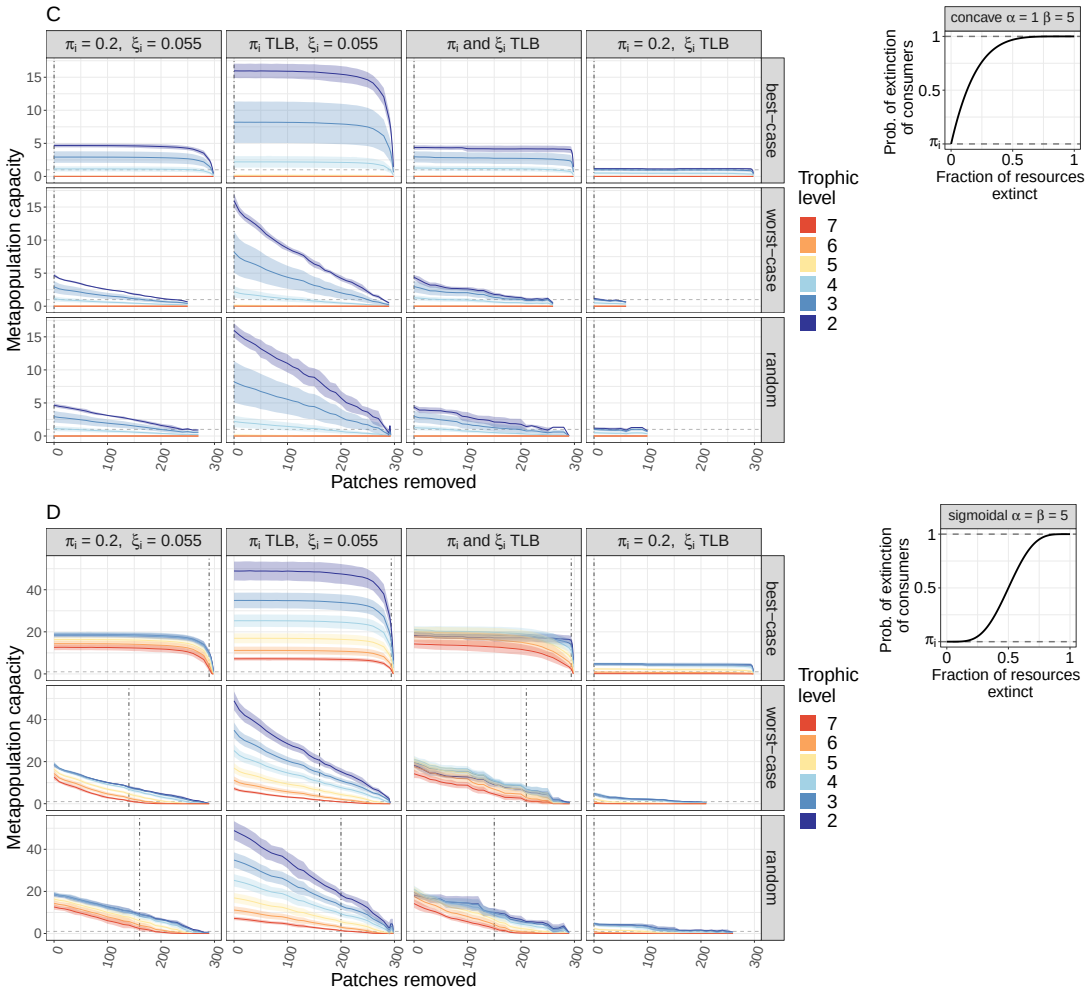

Figure S15: Figure continued.

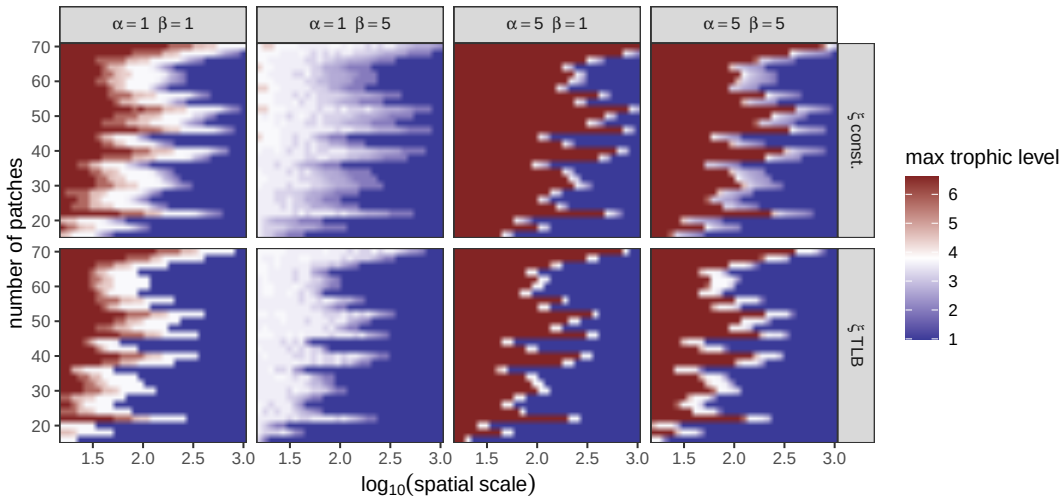

Figure S16: The maximum number of trophic levels (colors) persisting on a landscape with different numbers of patches (ordinate) and average distance between them (abscissa). The web used, which has 50 basal and 350 consumer species, is the same as in Figure S5. Landscapes were generated just like before, by randomly placing the appropriate number of patches in the unit square. In the top row, each species has an identical dispersal parameter ξ (equal to the spatial scale indicated along the abscissa), while in the bottom row, they were trophic level-based (increasing linearly with trophic level such that their average was equal to the spatial scale parameter). Columns show various parameterizations of the consumer response to prey loss (linear, convex, concave, and sigmoid). The results are qualitatively identical to Figure S2 in Ryser *et al.* (2019): there is a strong dependence of the maximum attainable trophic level on the spatial scale, and a weaker one on the number of patches.

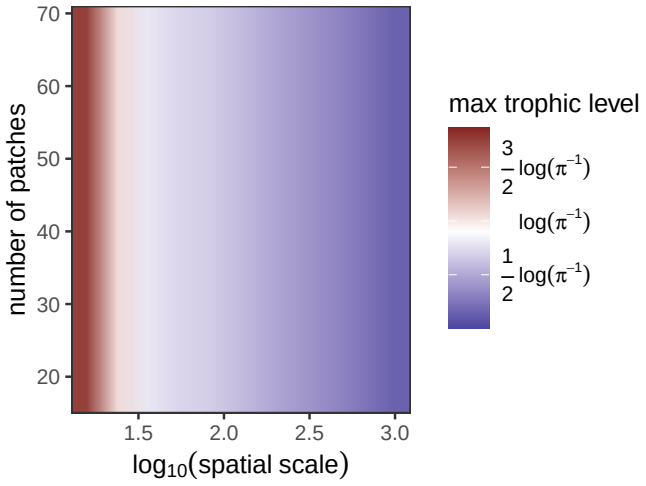

Figure S17: Analytical approximation of the expected maximum number of trophic levels (colors), given species' dispersal ability (abscissa) and the number of patches in the landscape (ordinate). The heat map is based on the approximation $T \approx \lambda_M \log(\pi^{-1})$ (Eq. S57), with the leading eigenvalues of the landscapes explicitly calculated based on their associated dispersal matrices.

To determine the best-case/worst-case link removal sequences, we chose links contributing the least/most to a local change of the basal species' metapopulation capacity. Since this metapopulation capacity is the leading eigenvalue of the matrix $A_i^{kl} = -M_i^{kl}/\log(1-\delta_i^k)$ (Eq. S11), we can apply standard eigenvalue sensitivity analysis to find the links contributing the least/most to the metapopulation capacity (Caswell 2001, ch. 9). This tells us that

$$\frac{\partial \lambda_i}{\partial A_i^{kl}} = \frac{v_i^k w_i^l}{\sum_{m=1}^{N} v_i^m w_i^m} , \tag{S96}$$

where λ_i is the metapopulation capacity of species i, v_i^k is the kth entry of its corresponding left eigenvector, and w_i^l the lth entry of the corresponding right eigenvector. Since the matrix A_i^{kl} has all positive entries, its leading eigenvectors have purely real and positive entries due to the Perron-Frobenius theorem. We numerically determine the right-hand side of Eq. S96, and sequentially delete the links corresponding its smallest entries (best-case scenario) or largest entries (worst-case scenario). More precisely, since we are removing links symmetrically, we remove links with the smallest/largest average entry $(v_i^k w_i^l + v_i^l w_i^k)/2$.

Since there are many links in a landscape (with N patches, there are $N(N-1)/2$ links; for $N = 300$, we have 44850 of them), we remove 1500 links in one iteration, and then re-calculate the sensitivity matrix via Eq. S96 using the updated matrix A_i^{kl} (from which certain links have already been deleted). The sensitivity formula is only accurate for small perturbations, so removing 1500 links at a time is somewhat crude but still produces consistent results. As seen in Figure S18, the results are almost the same as with patch removal, with one important qualitative difference: the random link removal scenario now lies about mid-way between the best- and worst-case ones, instead of being as bad as the worst-case scenario.

S10 Transitioning from a regular grid of habitat patches to random landscapes

Here we highlight the importance of the spatial arrangement of patches across the landscape for our results. Instead of using random landscapes, we create a gradient of landscapes from one in which patches are arranged in a perfect two-dimensional grid, to completely random ones. We do this by creating a 18×18 patch grid, and then jiggling the position of each patch by adding a uniform random value to both their x- and y-coordinates. The range in which the random addition happens ranges from 0 (perfect grid) to ± 0.5 (perfectly random). Coordinate values over 1 and below 0 are wrapped around to appear on the other side of the landscape; e.g., an x-coordinate of 1.2 is treated as being 0.2. We then performed the same patch removal analysis as before on each of these landscapes, for the case of $\alpha = \beta = 1$ (linear consumer response to prey loss). We recorded, for each scenario and parameterization, the number of patches that must be removed for the species of a given trophic level to disappear. Results are shown in Figure S19. In sum, very regular grids of patches lead to more vulnerable species, with fewer patches needing removal to drive them extinct. As the landscapes transition from regular to random patch arrangements, we recover the results observed earlier.

This result demonstrates that landscape arrangement matters, and that highly regular landscapes are more vulnerable than random ones (the same was found by Grilli *et al.* 2015). The explanation for this is that random landscapes have, by chance, clusters of close-by patches, boosting species' metapopulation capacities. Note though that there are diminishing returns: beyond a point, making the landscapes even more aggregated no longer enhances persistence, as seen from the figure.

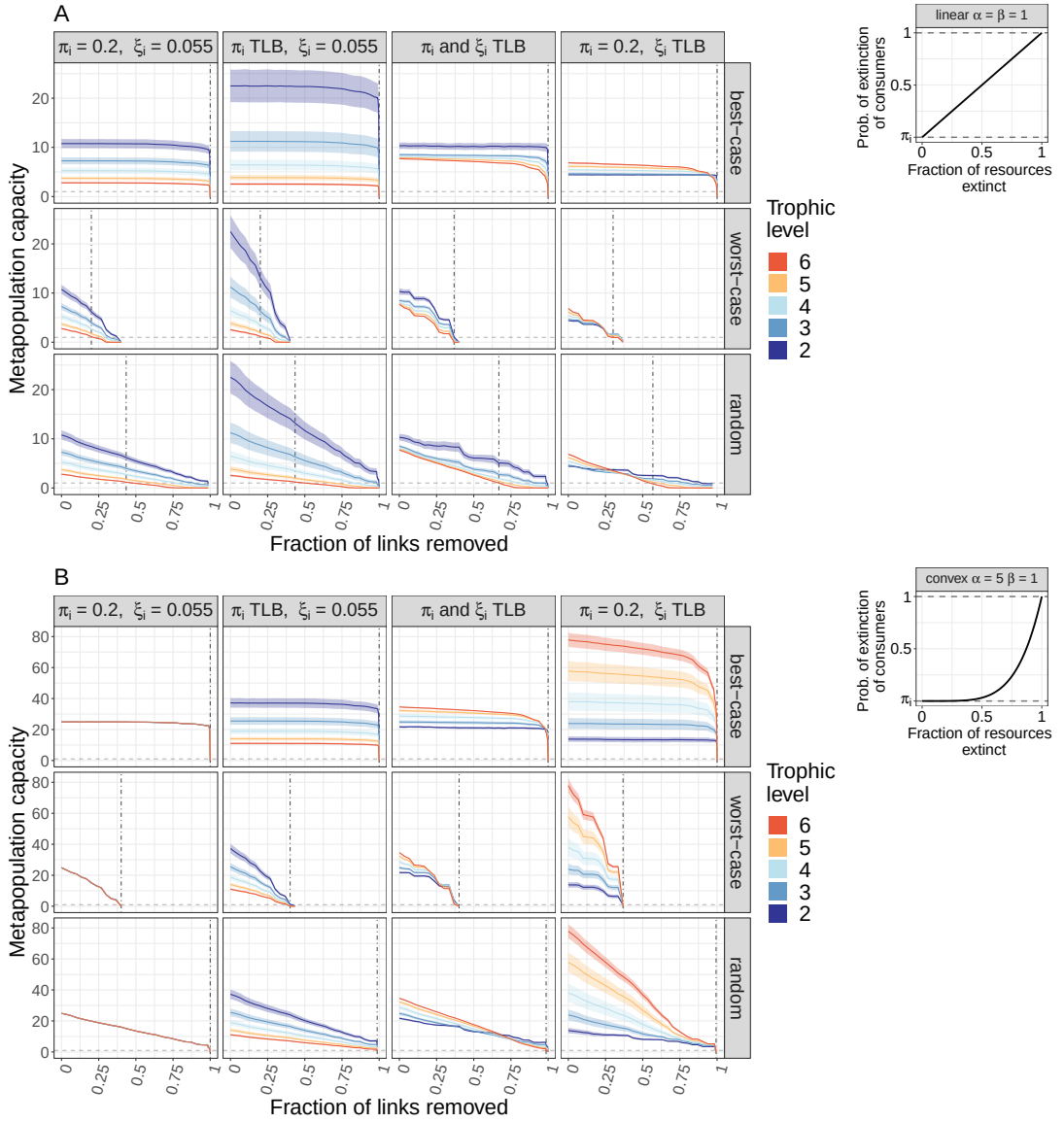

Figure S18: As Figure 2 in the main text, except removing links between pairs of patches, instead of the patches themselves. The abscissa shows the fraction of links removed, out of all possible ones—with N habitat patches, this number is $N(N-1)/2$. Results are very similar to those of patch removal, with one important qualitative difference: the worst-case scenario, instead of being as bad as the worst-case one, is now in between the two extremal scenarios.

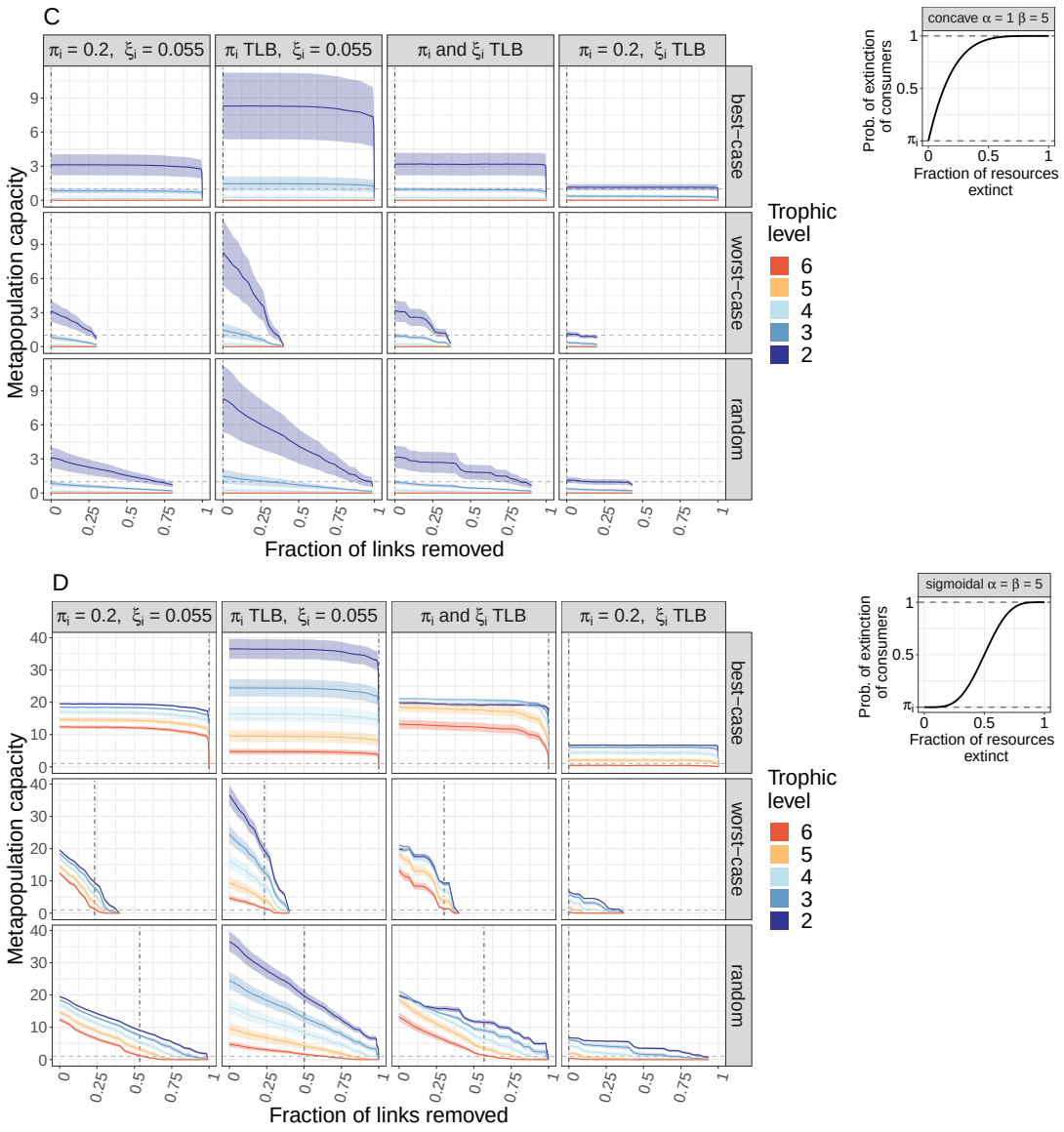

Figure S18: Figure continued.

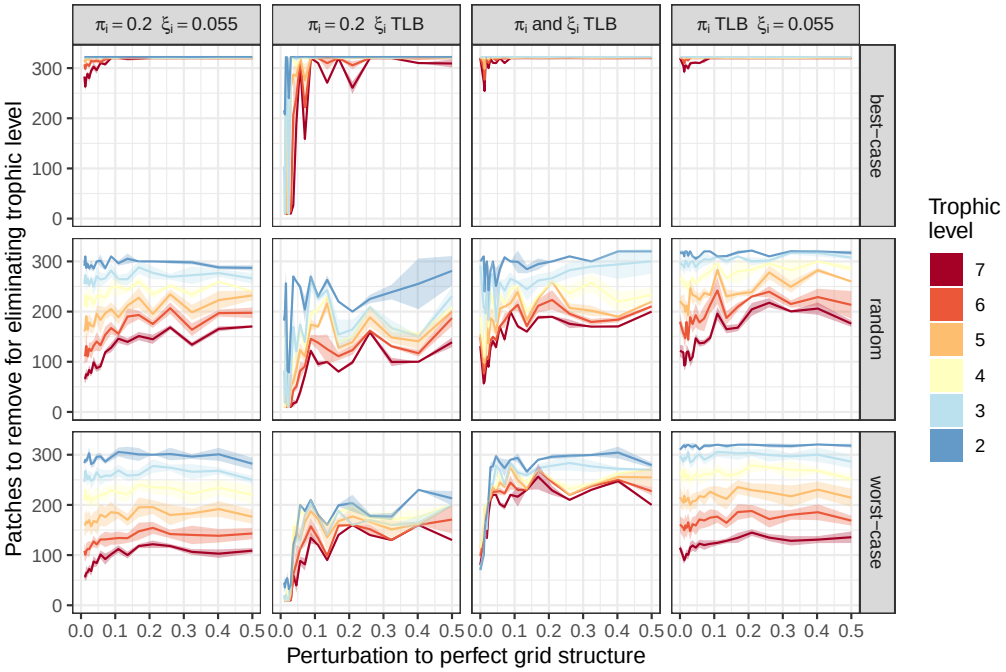

Figure S19: The number of patches (ordinate) which, when removed, cause the extinction of species at various trophic levels (colors, with the lines showing the mean across the species of each trophic level, and the bands around it the one-sigma standard deviations). The abscissa shows how far the patches of the landscape are from being perfectly arranged in a grid (0: perfect grid; 0.5: random landscape). Otherwise, layout is as in Figure S5. We see that more grid-like landscapes lead to lower persistence thresholds, but that landscapes above a perturbation level of about 0.2 behave as if they were completely random.

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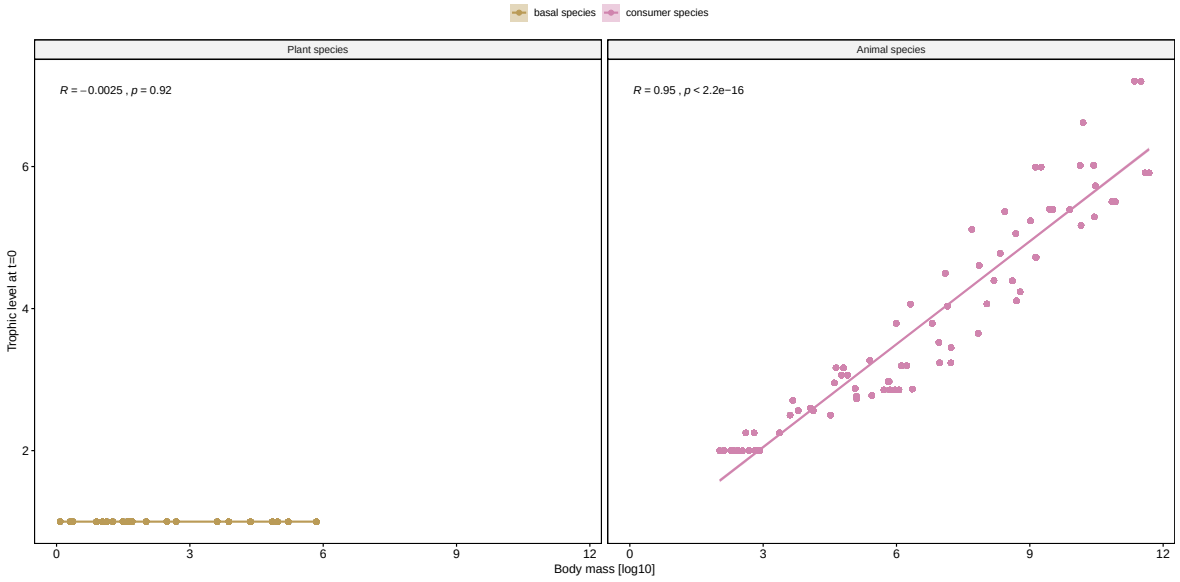
D

Supplementary Information for Research Chapter 3

Johanna Häussler, Remo Ryser & Ulrich Brose. ”Invasive spread in meta-food-webs depends on landscape structure, fertilization and species traits”.

(a)



(b)

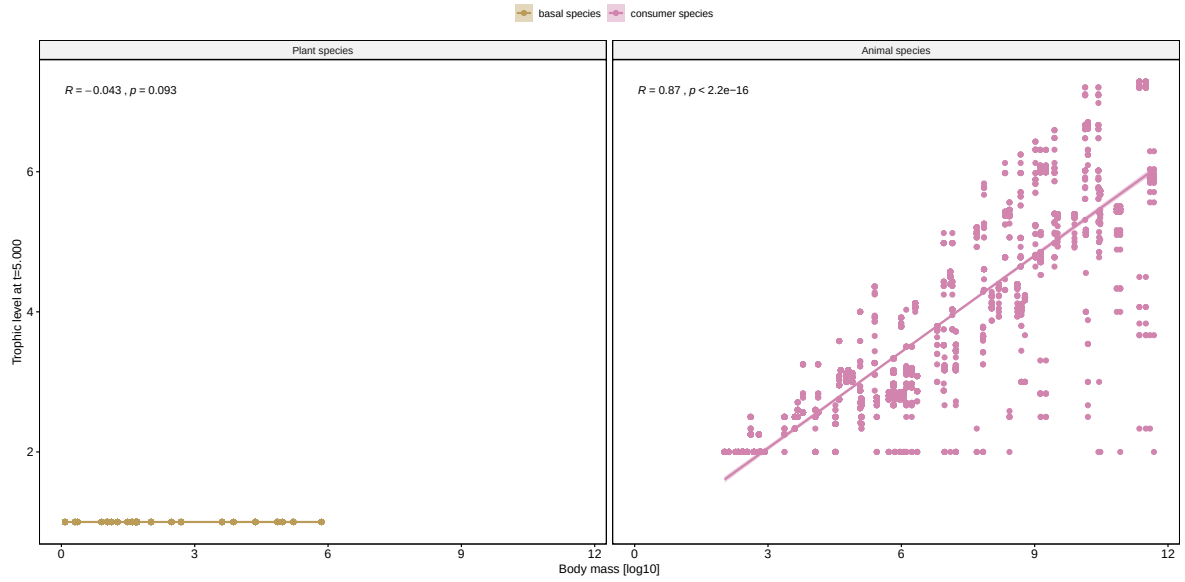


Figure D.S1: Relationship between body mass m_i ($\log_{10}$-transformed) and trophic level at $t = 0$, separately for plant species (left column, green, trophic level = 1) and animal species (right column, blue, trophic levels > 1).

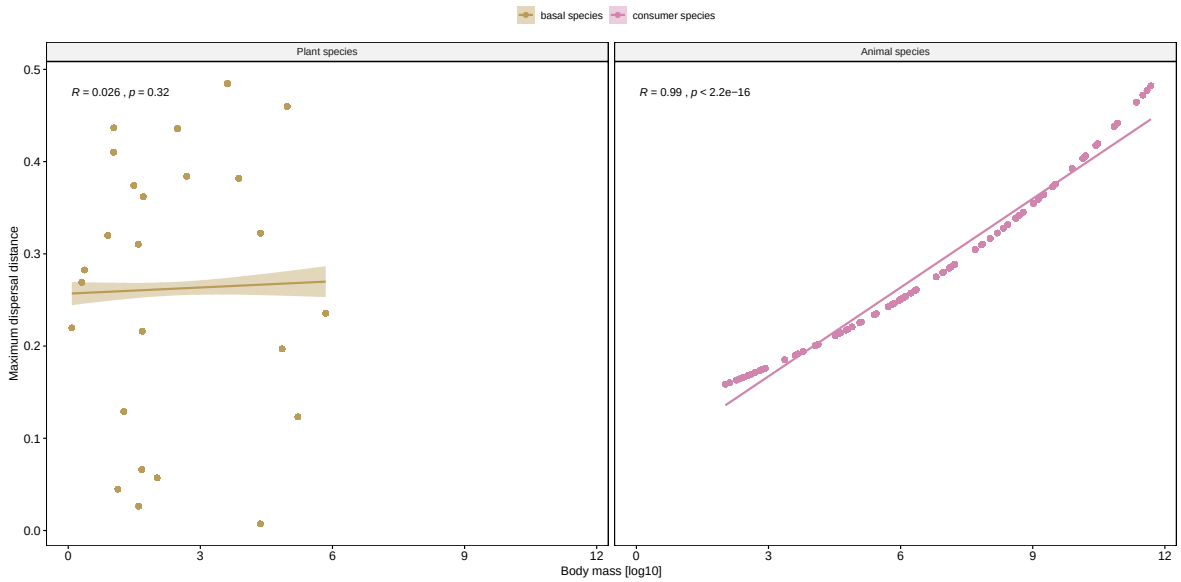


Figure D.S2: Relationship between body mass, m_i ($\log_{10}$-transformed), and maximum dispersal distance, δ_i, separately for plant species (left column, yellow, drawn at random) and animal species (right column, pink, determined by Eq. T2.1, Table 2, main document.

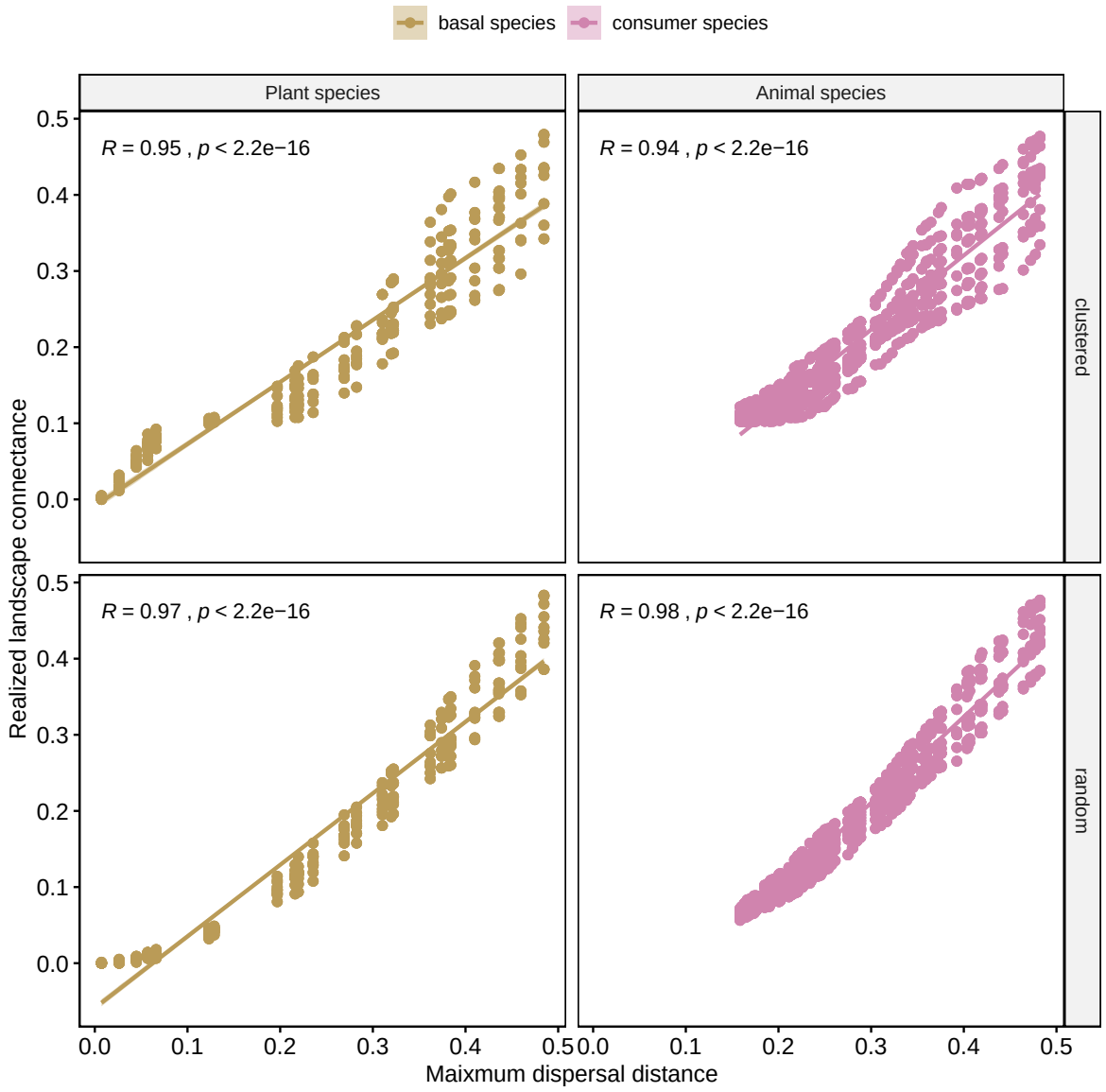


Figure D.S3: Relationship between maximum dispersal distance, δ_i, and realized landscape connectance, separately for plants (left column, yellow) and animals (right column, pink). Rows indicate landscape structure).

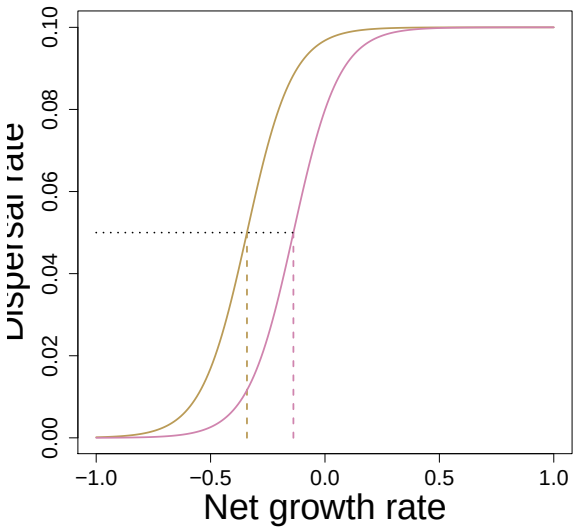


Figure D.S4: Function showing the per capita dispersal rate, d_i, for plants (yellow) and animals (pink), where x_i marks the inflection point for each species i determined by the metabolic demands per unit biomass of species i (differing between plants and animals), the shape parameter $b = 10$, determining the slope, and $a = 0.1$, determining the maximum emigration rate (main document, Table 2, Eq. T2.2). For the purpose of illustration, we set $x_i = 0.314$ for animals and $x_i = 0.1384$ for plants.

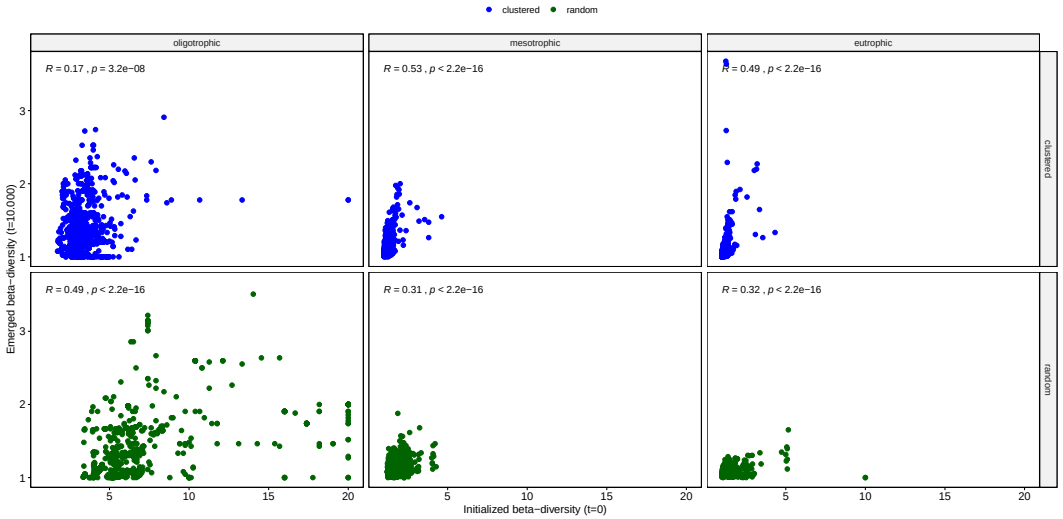


Figure D.S5: Relationship between the β-diversity we initialized at $t = 0$ (see main document, Section 2, *Invasion simulations*) and the β-diversity that emerged by numerically simulating the feeding and dispersal dynamics of the (invaded) meta-food-web for 10.000 time steps, separately for each landscape type. Columns indicate nutrient supply scenario, rows landscape structure (clustered: blue; random: green).

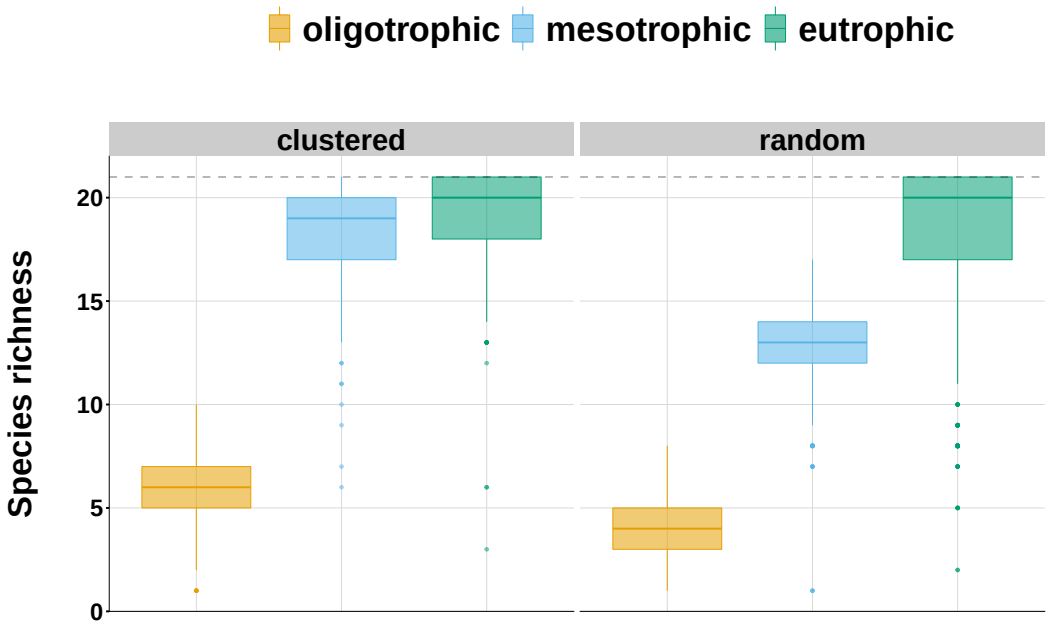


Figure D.S6: Effects of landscape properties on species richness. The dashed line indicates the maximal possible number of species in the invaded meta-food-web ($S = 21$). Columns indicate the spatial configuration of habitat (clustered and random); colors different levels of nutrient supply. Species richness was evaluated post-simulation at time $t = 10.0000$, counting a species as extant when its biomass density exceeded the extinction threshold of 10^{-20}.

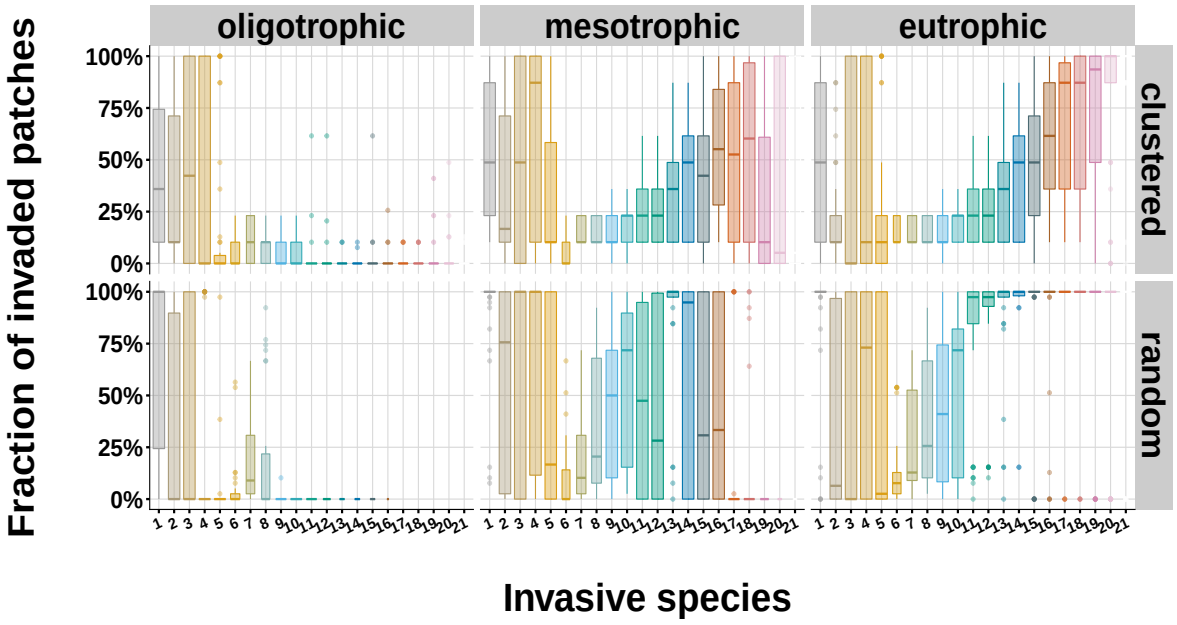
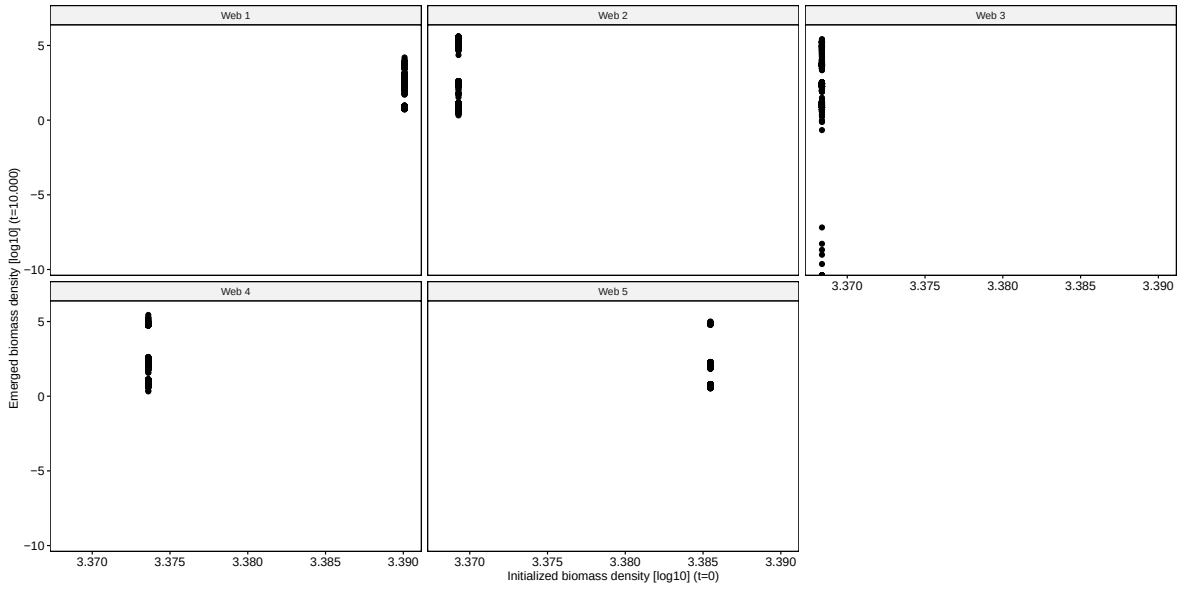


Figure D.S7: Invasive spread (measured as the fraction of invaded patches) in landscapes varying in their spatial configuration of habitat and nutrient availability in response to invasive species. Columns indicate nutrient availability in a landscape; rows the spatial configuration of habitat. The fraction of invaded patches was evaluated post-simulation at time $t = 10.0000$, counting a patch as invaded when the biomass density of the invader exceeded the extinction threshold of 10^{-20}.

(a)



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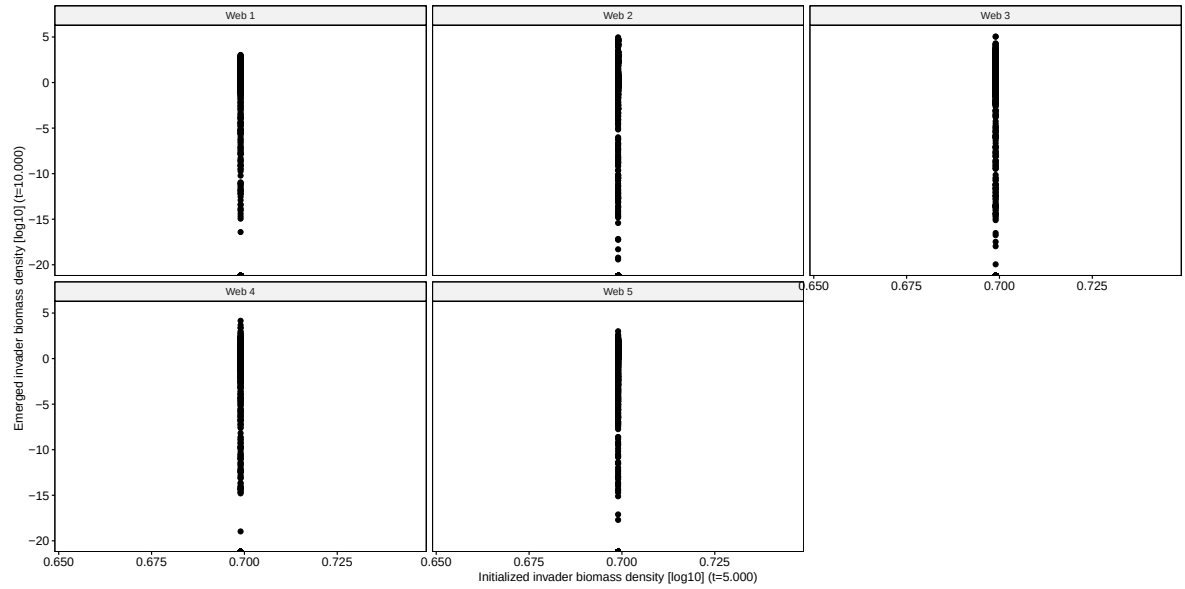

Figure D.S8: (a) Relationship between initialized biomass density of all species at $t = 0$ (native meta-food-web, $S = 20$) and emerged biomass density at $t = 10.000$ (invaded meta-food-web, $S = 20 + 1$). (b) Relationship between initialized invader biomass density at the time of introduction ($t = 5.000$) and its biomass density at $t = 10.000$, after simulating the feeding and dispersal dynamics of the invaded meta-food-web for 5.000 time steps.

E

Ehrenwörtliche Erklärung

Ich versichere, dass mir die geltende Promotionsordnung bekannt ist, ich die Dissertation selbstständig und ohne unerlaubte Hilfe Dritter angefertigt habe, keine Textabschnitte Dritter oder eigener Prüfungsarbeiten ohne Kennzeichnung übernommen habe und alle benutzten Hilfsmittel, persönlichen Mitteilungen und Quellen in der Arbeit angegeben habe. Alle Stellen, die inhaltlich oder wörtlich aus Veröffentlichungen stammen, sind kenntlich gemacht. Ich habe keine Hilfe einer kommerziellen Promotionsvermittlung in Anspruch genommen und Dritte haben weder unmittelbar noch mittelbar geldwerte Leistungen für Arbeiten erhalten, die im Zusammenhang mit dem Inhalt der vorgelegten Dissertation stehen.

Folgende Personen haben mich bei der Auswahl und Auswertung des Materials sowie bei der Herstellung der einzelnen Manuskripte unterstützt: Remo Ryser, Markus Stark, Björn C. Rall, Christian Guill, Anna Eklöf, György Barabás und Ulrich Brose. Nähere Angaben sind den Forschungskapiteln zu entnehmen.

Diese Dissertation lag noch nicht als staatliche oder andere wissenschaftliche Prüfungsarbeit einer Prüfungsbehörde vor und wurde bisher noch nicht veröffentlicht. Ich habe die gleiche, eine in wesentlichen Teilen ähnliche oder eine andere Abhandlung bei keiner anderen Hochschule oder anderen Fakultät als Dissertation eingereicht hat.

Johanna Katharina Häußler

Leipzig, den 13.12.2020